SALPA FUSIFORMIS CUVIER AND
RELATED SPECIES

By

P. FOXTON

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(Plates I–II and Text-figs. 1–10)

INTRODUCTION

THIS paper represents the first part of a study of the salps of the Southern Ocean, and is a contribution to the National Institute of Oceanography's studies of the distribution of oceanic organisms and the factors that govern them.

Previous studies, which have described the distributions and life-histories of species of Chaetognatha (David, 1955, 1958) and Euphausiidae (Baker, 1959; Marr, in press) show that even in an area of relatively simple oceanic circulation with well-defined water masses, such as the Southern Ocean, there is more regional differentiation in plankton distribution than had hitherto been supposed. Furthermore, these regional differences become more apparent when it is possible to ascertain the range of variation between species, subspecies and local races.

The salps commend themselves to a special study because, apart from the work of Michael (1918) and Yount (1958), little attention has been paid to the relationship between their life-history and their environment in spite of the fact that they were one of the earliest planktonic groups to be described. In the Southern Ocean the salps are of especial interest because they occur at certain seasons in dense concentrations or swarms and, as they are primarily herbivorous, must play an important role in grazing down the phytoplankton, competing where distributions overlap, with such other key herbivores as *Euphausia superba*.

The common salp of the subantarctic and antarctic zones of the Southern Ocean has in the past been assumed to be *Salpa fusiformis aspera*, a variety or subspecies, characterized by a serrated test, of the type *S. fusiformis*. Confusion in the literature and discrepancies between published descriptions and specimens from the Southern Ocean made it necessary at the outset to examine in detail the taxonomy of the salp common in our collections and to establish the validity or otherwise, not only of previous identifications, but of *S. fusiformis aspera* as a subspecies, form or extreme variant of *S. fusiformis*.

Fortunately a large collection of material was available for study mainly from the Southern Ocean but also to a lesser extent from the Southern Indian, North Atlantic and South Atlantic Oceans. I have also, by the kindness of workers in other laboratories, been able to extend the geographical range of specimens examined into areas not represented in the plankton collections of the National Institute of Oceanography.

The results of this study show that the differences between *S. fusiformis* and the variety *S. fusiformis aspera* are greater than had been previously supposed. Within what I shall refer to as the 'fusiformis group' there has been a confusion of four species, three of these being hitherto variously known as *S. fusiformis aspera*. Morphological differences and features of geographical distribution allow the four species *S. fusiformis*, *S. aspera*, *S. thompsoni* and *S. gerlachei* to be recognized. Two of these species, *S. thompsoni* and *S. gerlachei*, are limited in their distribution to the Southern Ocean and it is with the ecology of these that a later paper will be primarily concerned. It was felt, however, that it

would be useful at this stage to present the systematic results in advance, particularly since there has been such confusion and divergence of opinion regarding the relationship between *S. fusiformis* and *S. fusiformis aspera*.

ACKNOWLEDGEMENTS

MATERIAL AND METHODS

This paper is based for the most part on material collected by ships of the Discovery Committee and subsequently the National Institute of Oceanography. As the ultimate aim of the work was a quantitative appraisal of an animal's distribution in time and space in relation to its life-history, I have used plankton samples taken with a standard net fished in a standard manner. In this paper only a small part of the total data—that relating to the systematic results—will be used.

Most of the material was collected with a 1-metre stramin net towed obliquely (N 100 B) or horizontally (N 100 H) at stations which were selected, from a vast number available,. to give as complete a geographical coverage of the Southern Ocean as possible. It was soon realized that the subantarctic and antarctic data should be compared with that from other oceans, and so where lines of stations have extended north of the subtropical convergence (indicated by a dotted line in Text-fig. 10, p. 28) use has been made of samples collected at them irrespective of the gear used. Such samples include those taken with the 2-metre stramin net fished obliquely (TYFB) or horizontally (TYFV) and use has also been made of material collected in the North Atlantic with the Isaacs–Kidd Midwater Trawl. While not relevant to this paper, full descriptions of the 1-metre and 2-metre nets and their method of use may be found in Kemp, Hardy and Mackintosh (1929), while the Isaacs–Kidd Midwater Trawl is described by Isaacs and Kidd (1953).

I have, in addition, been able to examine specimens collected with a variety of gear from areas not represented in the Discovery Collections. These include specimens from the eastern and central Pacific, Japan, Bay of Biscay, and Iceland. I have also been able to augment the Discovery Pacific stations with material collected quite independently by the Norwegian 'Brategg' Expedition of 1947–48.

All the measurements on which this study is based were made on specimens preserved in 5–10% neutral sea-water formalin. As the period of preservation prior to examination varies from a few months to 30 or so years some shrinkage can be assumed to have taken place. A few specimens, how-

ever, which were originally examined alive, or just a few minutes after preservation in 1951, showed no significant change in size when re-examined in 1959. It thus seems safe to assume that the effects of shrinkage due to preservation, at least in so far as they affect the morphological characters used in this study, are negligible.

The number of aggregate and solitary individuals of each species in each sample was counted while the size composition of each form was determined by length measurements. The stage of development of the embryo or stolon was assessed by detailed examination of the oozoid (= solitary) and blasto-zooid (= aggregate) with a low-power stereomicroscope. These measurements and counts result in data that will form the basis of a later paper on life-history and distribution. The present work is concerned with detailed structure in so far as it relates to the taxonomy of the animals, and this depends on the detailed examination and measurements to be described.

In many previous works devoted to the description of collections of salps measurements of length are given often without the points of reference from which the measurements were made. This seems to be of importance, because while some authors distinguish between measurements that include the prolongations that often characterize the test, others do not, even though such extensions of the test may represent a large percentage of the total length. While strictly speaking the length of a specimen should be the distance between its anterior and posterior extremities such a measurement seems unsatisfactory when applied to the Salpidae. Firstly, the test is very variable in form not only between species but within species on account of age, natural wear and damage in the net, and, secondly, the test frequently becomes separated from the body n very ri h samples presumably through damage in the net, since salps are on the whole fragile animals. It thus seems more realistic to use measurements of length based on the body (or mantle; see Yount, 1954) rather than the test.

In the present study the following standard measurements are used:

total length, the distance between the anterior and posterior extremities of the test;

body length, the distance between the mouth and the atrial opening;

nucleus length, the nucleus (or alimentary canal) is typically ovoid in the species to be considered and so the measurement taken is the length of the major axis.

Throughout this paper all lengths quoted will refer to body length unless otherwise stated. It will be realized from the relative shape of the solitary and aggregate stages that in the former total length and body length approximate to each other while in the latter they may be very different. Lengths in all cases were measured to the nearest millimetre on a clear plastic graduated scale. With larger specimens, particularly of the solitary form greater than 50–60 mm. in length, the measurement is not assumed to be more accurate than ± 2 mm., owing to the extreme elasticity of the body especially in specimens that have become separated from their tests. However, this in no way invalidates conclusions drawn from such data which are always grouped for purposes of comparison into 5 or 10 mm. size groups.

The detailed examination of specimens was assisted by the use of aqueous stains. Toluidine blue (Yount, 1954) or methylene blue in dilute solution allowed the surface of the test (p. 22) to be seen in detail, and in some cases made visible denticulations on old worn tests that might well have been classed as smooth. Rose Bengale (Yount, 1954) injected either through the mouth or the atrial aperture into the body proved a useful method of seeing the arrangement of the body musculature, particularly in small specimens.

A low-power stereomicroscope proved adequate to see the structure of individual muscle bands and except in very small specimens it was possible to count the number of constituent fibres in each muscle (p. 15). Where necessary the widths of individual muscle bands (see p. 23) were measured with a graduated eyepiece.

The scheme of nomenclature followed in this paper is based on that described by Yount (1954) in which the test is described in terms largely formulated by Stiasny (1926), while the muscle notation follows that of Streiff (1908).

SYNONYMY AND PREVIOUS DESCRIPTIONS

It is proposed in this section to describe only those works that are relevant to a discussion of the synonymy of *Salpa fusiformis* and its related species, and in particular to the status of the serrated forms. For a detailed account of the taxonomy of the Salpidae in general, reference should be made to Metcalf (1918) or to Thompson (1948), who deals with the pelagic Tunicata as a whole.

It should be remembered that in the early nomenclature of the group, solitary and aggregate forms of the same species often acquired different names. For example, Cuvier (1804) gives the name *S. fusiformis* for the aggregate form of the species, while Chamisso (1819) calls the solitary form of the same species *S. runcinata*. With the realization, largely as a result of the work of Chamisso (1819), that the two forms were morphologically different stages in the life-history of a single species, the one sexual, the other asexual, the two names became linked by a hyphen. Thus the species became known as *S. runcinata-fusiformis* Chamisso-Cuvier (Krohn, 1846; Traustedt, 1885; Herdman, 1888). Subsequently it was considered by Ritter (1905) that the first name in the couplet should be that having priority and so the specific name became *S. fusiformis-runcinata* Cuvier-Chamisso. While many authors followed the lead of Krohn (1846), others, notably Apstein (1894b), foreshadowed modern usage in dropping the second name of the couplet, so making the species *S. fusiformis* Cuvier. In the following account of previous literature the nomenclature used is that of the author under discussion.

Herdman (1888) described from the Challenger collections the solitary form of a new species—*S. echinata*—which differed from *S. runcinata-fusiformis* Cuv.-Cham. in having a serrated test and in M. (body muscles) IV–IX being parallel. He failed, however, to recognize the aggregate form of the species, although it can be concluded from his remarks (pp. 76–7) with regard to variation in specimens of the aggregate form of *S. runcinata-fusiformis*, from the geographical location of his stations, and from his figures (Pl. VI, figs. 5–10) that he had a mixture of species in which such differences as I have taken to be specific were regarded as mere variations within the one species—*S. runcinata-fusiformis*.

Apstein (1894b) in tropical material found two specimens of a solitary form that agreed with Herdman's (1888) description of *S. echinata*. However, on the basis of an examination of the stolon of one of the specimens, buds of the aggregate form were found and figured (fig. 14) similar to the aggregate of *S. fusiformis* but differing in the slight lateral separation of M. IV and V. On the basis of their general similarity Apstein concluded that his specimens were variants of *S. fusiformis* that occurred only in the solitary form, and so called them *S. fusiformis* var. *echinata* (p. 15). It should be noted that both Apstein (fig. 14) and Herdman (fig. 7) figure specimens of the aggregate form with a lateral separation of M. IV–V, and in neither case is any significance attached to this morphological difference.

Ritter (1905) described specimens similar to those of Herdman (1888) and Apstein (1894b) which he called *S. fusiformis-runcinata* form *echinata*. Figures 14–15 (p. 68) are the best to that date of the solitary form, and show the serrations of the test in detail and the body musculature with M. IV–IX parallel. Ritter's specimens were larger than those of the type *S. fusiformis-runcinata* and so he considered *echinata* to be a 'well-marked style or form of the species associated with age'.

From a large collection, which included antarctic specimens, Apstein (1906) described (pp. 249–50) and figured (Pl. XXVI) well-serrated aggregate (fig. 4) and solitary (fig. 6) forms of *S. fusiformis* form *echinata*. Unlike previous descriptions of the serrated form the solitary is shown with M. VIII–IX medio-dorsally joined, while the aggregate is figured with a well-serrated test and M. IV–V not joined

laterally. Apstein's data covered a wide geographical range, and since the serrated form tended to occur in the colder waters (p. 269, figs. 5–6) he concluded that the form *echinata* was a cold-water variant of the type occurring in both aggregate and solitary form. Apstein, however, remarks (p. 250) that the differences between the form *echinata* and the type show great variation. This, together with the fact that the collection was from a wide geographical area, including subantarctic and antarctic material, suggests that there was a confusion of species. It will be shown later (p. 22) that the specimen of the solitary form (Text-fig. 6) is typical of a species limited in its distribution to the Southern Ocean, while the aggregate form (Text-fig. 4) shows characters associated with a species that occurs only in waters north of the subtropical convergence.

Farran (1906) in an oft-quoted paper described the serrated form in Irish waters from specimens of the aggregate stage. His statement that the musculature was the same as that of the type refers to specimens of the aggregate stage only, but it has frequently been quoted as referring to the solitary form as well (Thompson 1948 p. 158).

The serrated form of *S. fusiformis* has subsequently been described from collections made by most expeditions, and references are to be found in Apstein (1908); Ihle (1910, 1911, 1912); and Murray and Hjort (1912), and others. Ihle (1911, p. 587) used for the first time the name *S. fusiformis aspera* to designate this serrated form.

From a small collection of material collected by the Belgica Expedition van Beneden and Selys-Longchamps (1913) described in a rarely quoted paper a new variety of *S. fusiformis* which they called *S. fusiformis Gerlachei*. Their description, based on one specimen each of the solitary and aggregate forms, is most thorough and detailed, and a comparison is made between their specimens and Herdman's (1888) and Ritter's (1905) descriptions of *S. echinata* and *S. fusiformis-runcinata*. The solitary form of *S. fusiformis Gerlachei* differs from *S. echinata* in having M. VIII and IX joined and having a highly serrated test with a medio-dorsal serrated ridge. Some of the differences they describe, such as the lack of a 'cephalic projection' in the aggregate form, are probably variations attributable to wear or damage but the major characters of muscle arrangement and test structure they found incompatible with the published descriptions of *S. echinata* and *S. fusiformis-runcinata*. They suggest (p. 119) that these differences are characteristic of a form, variety or species endemic to the part of the Antarctic from which they came, although they agree that on such limited material the possibility of individual variation cannot be ruled out.

Metcalf (1918) in his classic paper on the Salpidae of the Philippines concludes that the specimens of *S. fusiformis aspera* in his collection showed a complete intergradation between smooth and the most spinose test. His figure of the solitary form is of interest because it seems to combine the test characters of Ritter (1905, fig. 14) based on specimens from the San Diego region, and the musculature of Apstein (1906, fig. 6) based on antarctic specimens—a combination not found in any of the specimens to be described in this paper.

Sewell (1926, p. 76) reviews briefly previous records of *S. fusiformis aspera* and their interpretation and concludes that 'it seems impossible to justify any separation, even as a distinct form, of those with spinose test from those with a smooth one, though it is possible that Ritter and Farran are right in their belief that the spinose character is a mark of age'. This view is favoured by Thompson (1948) while Yount (1954) goes further and groups all the variants together as *S. fusiformis*.

The works described above are those relevant to the problem of the serrated form of *S. fusiformis* and the various conclusions of the authors cited may be summarized as follows.

(1) New species: Chamisso, 1819; Herdman, 1888.

(2) A subspecies (of which there may be others): van Beneden & Longchamps, 1913.

(3) Cold-water form; Apstein, 1906.

(4) Old-age variant: Ritter, 1905; Farran, 1906.

(5) No recognizable variety or form: Sewell, 1926; Yount, 1954.

It is perhaps not surprising in view of these differing conclusions that the overall picture of the geographical range of *S. fusiformis* extends from 60° N. to 65° S. (Thompson, 1948). Few, however, of the above papers are based on adequate subantarctic and antarctic material and it is significant that where specimens were available, well-serrated animals are described in which the solitary form has M. VIII and IX joined dorsally (Apstein, 1906; van Beneden, 1913), while in some cases specimens of the aggregate form are described in which M. IV and V are joined laterally (Herdman, 1888; van Beneden, 1913).

It will be realized from the above that previous authors have attached varying taxonomic importance to different morphological features. When any one of these features, such as the external character of the test, has been considered on its own, such differences as occurred, particularly in those collections of material that cover a wide geographical range, have invariably been attributed to individual variation within a single species. The data to be presented here will show that it is possible by considering variation in a complex of characters to distinguish four species. These species have been variously confused in the literature of the group.

DESCRIPTION OF THE SPECIES
Salpa fusiformis Cuvier, 1804 (Text-fig. 1 a, b)

Salpa maxima variety Forskål, 1775.

Salpa fusiformis Cuvier, G., 1804, *Ann. Mus. Hist. Nat.*, An. XII, Tome 4, pp. 360–82, pl. 68; Apstein, 1894b, 1901, 1906; Farran, 1906; Streiff, 1908; Ihle, 1910, 1935; Sigl, 1912; Bomford, 1913; Metcalf, 1918; Sewell, 1926, 1953; Thompson, 1948; Yount, 1954 (part); Bernard, 1958; Fagetti, 1959.

Salpa runcinata Chamisso, 1819; Brooks, 1893.

Salpa maxima Meyen, 1832.

Biphora depressa Sars, 1829.

Biphora tricuspidata Sars, 1829.

Salpa runcinata-fusiformis Krohn, 1846; Traustedt, 1885; Herdman, 1888; Apstein, 1894a.

Salpa fusiformis-runcinata Ritter, 1905; Ritter and Byxbee, 1905 (part).

Salpa fusiformis fusiformis Ihle, 1912; Stiasny, 1926.

Salpa fusiformis f. typica Michaelson, 1915.

SOLITARY FORM (Text-fig. 1 a)
(based on the examination of fifty-three specimens)

EXTERNAL APPEARANCE. Elongate, with a slightly convex anterior and a squarely cut off posterior. In section the anterior is subcylindrical with a flattened dorsal surface, while the posterior is triangular. The mouth and the atrial apertures are terminal.

TEST. Smooth, firm and transparent. Thin, except where thickened to form characteristic ridges. From the posterior dorsal edge, starting at two spinose processes of the test there are the left and right dorsal limiting ridges which, proceeding forward, soon divide into outer and inner branches. Lateral ridges, also originating in posterior processes, form the edges to the dorsal surface. A ventro-lateral ridge runs below each dorsal edge while posteriorly there is a well-marked keel-like mid-ventral ridge which, directed forward, divides to form two ventral limiting ridges.

BODY MUSCLES. Nine body muscles. M. I–III and M. VIII–IX converge and fuse medio-dorsally. M. IV–VII are parallel.

MUSCLE FIBRES. Mean number 29·4 ± 1·4 for M. IV, based on forty-eight specimens. See pp. 15–21 for explanation.

ALIMENTARY CANAL. Compact, oval nucleus.

STOLON. Proceeds forward, turning left at about the level of M. III, to proceed back emerging from the test in front of the nucleus.

LENGTH. Up to 45 mm.
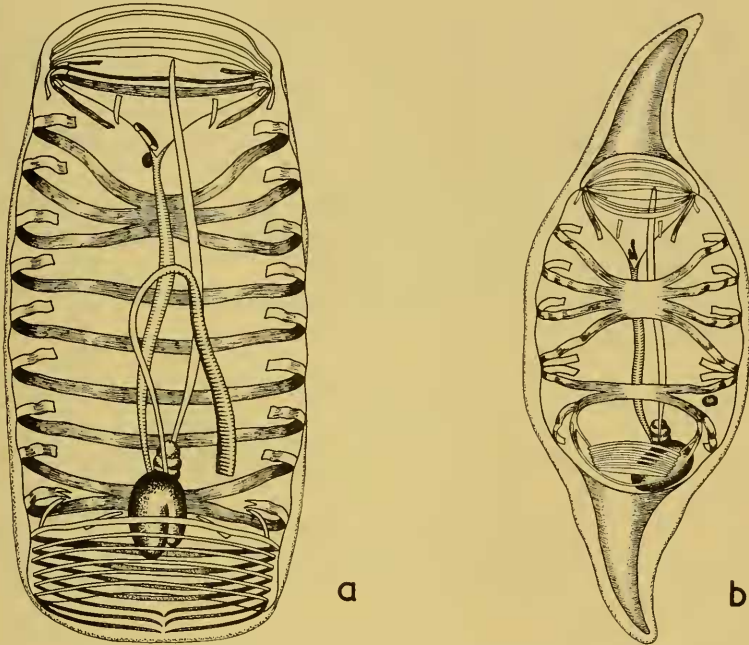
Text-fig. 1. *S. fusiformis* (*a*) Solitary form, ventral view. Length 20 mm. (*b*) Aggregate form, dorsal view. Length 20 mm. (From Thompson, 1948.)

AGGREGATE FORM (Text-fig. 1*b*)

(Based on the examination of forty-eight specimens)

EXTERNAL APPEARANCE. Body barrel shaped with conical anterior and posterior protuberances of the test which are typically long in relation to the body, giving it a slight asymmetry* and an elongate, fusiformis appearance.

TEST. Smooth, firm, transparent with no obvious ridges.

BODY MUSCLES. Six body muscles. M. I–IV and M. V–VI fuse dorsally, thus forming two groups. M. IV–V approach and join laterally.

MUSCLE FIBRES. Mean number 51·8 ± 1·4 for the total of M. I–VI, based on 45 specimens. See pp. 15–21 for explanation. Approximate mean number of fibres per muscle of 8·6.

ALIMENTARY CANAL. Compact, oval nucleus with its major axis lying to the right. Pale green in living specimens.

* *Note.* In *S. fusiformis* and in the three other species to be described the protuberances or processes of the test are asymmetrical, the anterior being to the right, the posterior to the left, or vice versa depending on the zooid's original position in the stolon.

EMBRYO. Single embryo, behind M. V at its point of lateral fusion with M. IV.

LENGTH. Up to 25 mm.

DISTRIBUTION OF *S. FUSIFORMIS*. Recorded by other workers in nearly all oceans (see Thompson, 1948). Present data demonstrate that the southern limit to its distribution is the region of the subtropical convergence. Data are insufficient to define its northern limit but it has been recorded at a station in 63° 51′ N., 16° 20′ W., and also round the N. Cape of Iceland in September 1957 (Fraser, 1959).

Salpa aspera Chamisso, 1819 (Pl. I)

Salpa aspera Chamisso, A. von, 1819, De Animalibus quibusdam e classe Vermium Linnaeana, Fasc. 1, De Salpa, 24 pp., Pl. 1 (Berolini).

Salpa echinata Herdman, 1888.

Salpa runcinata-fusiformis Herdman, 1888 (part).

Salpa runcinata-fusiformis var. *echinata* Apstein, 1894a.

Salpa fusiformis var. *echinata* Apstein, 1894b; Apstein 1906 (part), 1908; Ihle, 1910.

Salpa fusiformis-runcinata form *echinata* Ritter, 1905; Ritter and Byxbee, 1905.

Salpa fusiformis-runcinata Ritter and Byxbee, 1905 (part).

Salpa fusiformis form *aspera* Ihle, 1911; 1935; Metcalf, 1918; Sewell, 1926; Thompson, 1948.

Salpa fusiformis Yount, 1954 (part).

SOLITARY FORM (Pl. I*a* and *c*)
(Based on the examination of nine specimens)

EXTERNAL APPEARANCE. Similar to *S. fusiformis*, with more convex anterior. Posterior squarely cut off with pronounced spinose processes.

TEST. (Pl. I*c*) Serrated. Thin except for the thickened ridges which are similar in number and disposition to *S. fusiformis*. Ridges characterized by denticulations of the test which give a serrated appearance. Posteriorly the serrated ridges extend to pronounced spinose processes of the test. As in *S. fusiformis* there are ten ridges defined as follows:

(a) Four dorsal-limiting ridges,

(b) Two dorsal-lateral ridges,

(c) Two ventro-lateral ridges,

(d) Two ventral ridges which originate posteriorly as a single mid-ventral ridge.

I shall refer to this arrangement of serrated ridges as 'simple'.

BODY MUSCLES. Nine body muscles. M. I–III converge and fuse dorsally. M. IV–VII are parallel. M. VIII–IX may approach but do not fuse medio-dorsally.

MUSCLE FIBRES. Mean number 100·7 for M. IV, based on nine specimens.

ALIMENTARY CANAL. Compact oval nucleus.

STOLON. Proceeds forward to about the level of M. VII where, turning left, it doubles back following the edge of the nucleus and emerging through the test on the right side of the nucleus between M. VIII–IX. LENGTH. Up to 95 mm.

AGGREGATE FORM (Pl. I*b*)
(Based on the examination of twenty-nine specimens)

EXTERNAL APPEARANCE. Body barrel shaped with conical anterior and posterior protruberances of the test. The latter show great variation in both their shape and length. None of the specimens showed the 'fusiform' appearance so characteristic of *S. fusiformis*.

TEST. Serrated. Denticulations irregular in their distribution.

BODY MUSCLES. Six body muscles. M. I–IV and M. V–VI fuse dorsally to form two dorsal muscle groups. M. IV–V approach laterally but do not fuse.

MUSCLE FIBRES. Mean number 194·1 for the total of M. I–VI, based on twenty-nine specimens.

ALIMENTARY CANAL. Compact oval nucleus.

EMBRYO. Single, as in *S. fusiformis*.

LENGTH. Up to 60 mm.

DISTRIBUTION OF *S. ASPERA*. Present data show its occurrence north of the subtropical convergence in Atlantic, Pacific and Indian Oceans.

Yount (1954, pp. 303–4) has drawn attention to the similarity between *S. maxima* Forskål and the serrated form of *S. fusiformis* (= *S. aspera*) and suggests that these species may have been confused in the literature. Specimens of the aggregate form of *S. maxima* examined in the course of the present study have differed from *S. aspera* in having a most pronounced bulbous thickening of the test, ventral to the nucleus; while the solitary form is quite distinct in the absence of dorsal fusion of M. I–III, M. I–IX being in fact more or less parallel (see Thompson, 1946, Pls. 68 and 69). Spinose or serrated specimens of *S. maxima* have not occurred so far in the collections examined and the serrated specimens of this species figured by Yount (ibid. p. 301, fig. 13 and p. 302, fig. 14) I consider likely to be *S. aspera*.

Salpa thompsoni sp.nov. (Pl. II)

[?] *Salpa antarctica* Meyen, 1832.

Salpa echinata Herdman, 1888 (part).

Salpa runcinata-fusiformis Herdman, 1888 (part); 1910.

Salpa fusiformis var. *echinata* Apstein, 1906 (part).

Salpa runcinata-fusiformis var. *echinata* Herdman, 1910 (part).

Salpa fusiformis aspera Mackintosh, 1934; Hardy and Gunther, 1935.

HOLOTYPE. A specimen of the solitary form 71 mm. long taken in a 1 m. net towed obliquely (N 100 B) between 89 m. and the surface at Discovery station 2144, 48° 04·3′ S., 101° 07·2′ E. on 11 December 1937.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.5.

BODY PROPORTIONS. Total length 75 mm., body length 71 mm., nucleus length 15 mm.

MUSCLE-FIBRE NUMBER. 89 fibres in M. IV.

STOLON. Stolon with two fully differentiated blocks of buds:

<p style="text-align:center">Block 1. 144 buds, blastozooids 3 mm. long
Block 2. 230 buds, blastozooids 1 mm. long.</p>

No evidence that previous release of buds has occurred (see p. 25). Stolon extends forward to level of M. V.

ALLOTYPE. A specimen of the aggregate form 20 mm. long taken in a 1 m. net towed obliquely (N 100 B) between 91 m. and the surface at Discovery station 1906, 53° 54·6′ S., 63° 58·1′ W. on 30 November 1936.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.6.

BODY PROPORTIONS. Total length 34 mm., body length 20 mm., nucleus length 5 mm.

MUSCLE-FIBRE NUMBER. 188 fibres for the sum of M. I–VI counted along the right side.

EMBRYO. Single oozoid present.

PARATYPES. Ten specimens of the solitary form taken in a 1 m. net towed obliquely (N 100 B) from 122 m. to the surface at Discovery station 2574, 47° 59·9′ S., 19° 56·2′ E. on 3 February 1939.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.7.

Ten specimens of the aggregate form taken in a 1 m. net towed obliquely (N 100 B) from 100 m. to the surface at Discovery station 2087, 44° 22·1′ S., 23° 31′ E. on 17 November 1937.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.8.

SOLITARY FORM (Pl. II a and c)

(Based on the examination of ninety-two specimens.)

EXTERNAL APPEARANCE. Elongate. Similar to *S. aspera* but more heavily serrated.

TEST (Pl. II c). Heavily serrated, firm, with thickened areas forming pronounced serrated ridges. Number and disposition of lateral and ventral ridges is similar to *S. aspera* but dorsal surface is more complex owing to a number of less pronounced ridges which I shall call secondary ridges to distinguish them from the more obvious principal ridges. Although not always immediately obvious the secondary ridges become particularly evident when stained with methylene blue (see p. 5).

The principal ridges are as follows:

(*a*) inner and outer dorsal limiting ridges,

(*b*) a dorsal-lateral ridge,

(*c*) a ventro-lateral ridge,

(*d*) posteriorly a single keel-like mid-ventral ridge which divides to form left and right branches or ventro-limiting ridges.

The secondary ridges are as follows:

(*e*) a medio-dorsal ridge extending for a greater part of the length of the body,

(*f*) a secondary dorsal-limiting ridge which runs between and parallel to the inner and outer dorsal-limiting ridges,

(*g*) a secondary dorso-lateral ridge which runs inside and parallel to the main dorso-lateral ridge,

(*h*) connecting the inner and outer branches of the dorsal-limiting ridges is a short transverse ridge at about the level of M. VIII.

I shall refer to this arrangement of serrated ridges as 'complex'.

BODY MUSCLES. Nine broad body muscles similar in their disposition to *S. fusiformis*. M. I–III fuse medio-dorsally. M. IV–VII are parallel. M. VIII–IX fuse medio-dorsally.

MUSCLE FIBRES. Mean number 93·2±2·8 for M. IV, based on 92 observations.

ALIMENTARY CANAL. Compact, oval nucleus.

STOLON. Similar to *S. aspera* but it extends anteriorly much further before doubling back on itself.

LENGTH. Up to 120 mm.

AGGREGATE FORM (Pl. II b)

(Based on the examination of one hundred and twenty-six specimens.)

EXTERNAL APPEARANCE. Body barrel shaped with conical anterior and posterior protuberances of the test. Great variation in body form. The anterior and posterior processes may be long, giving a typical 'fusiform' shape, or shortened.

TEST. Serrated, firm. From the anterior protuberance a dorsal serrated ridge runs posteriorly to form the right dorsal-lateral edge of the test. At about the level of the atrial orifice this serrated ridge divides to form a right ventral-lateral ridge which reconnects with the dorsal-lateral ridge at about the level of the nucleus. On the left side of the test there are left dorsal and ventral-lateral ridges which originate in the posterior protuberance. In well-serrated animals the disposition of these ridges is such as to give, as Herdman (1888, p. 76) remarked, an 'angular or somewhat prismatic appearance' to the test.

BODY MUSCLES. Six broad body muscles similar to *S. fusiformis*. M. I–IV and M. V–VI fused to form two dorsal groups. M. IV–V converge and join laterally.

MUSCLE FIBRES. Mean number $177\cdot7\pm3\cdot4$ for the total of M. I–VI, based on 126 specimens.

ALIMENTARY CANAL. Compact, oval nucleus.

EMBRYO. Single, in the same position as *S. fusiformis*.

DISTRIBUTION OF *S. THOMPSONI*. Restricted to the Southern Ocean. Does not occur north of the subtropical convergence. Circumpolar in moderate latitudes. In high latitudes restricted to Atlantic, Indian and Australian sectors.

Salpa gerlachei sp.nov. (Text-fig. 2)

Salpa runcinata-fusiformis var. *echinata* Herdman, 1910 (part?).

Salpa fusiformis var. *gerlachei* van Beneden and de Selys Longchamps, 1913.

HOLOTYPE. A specimen of the solitary form 56 mm. long taken in a 1 m. net towed horizontally (N 100 H) 5 m. below the surface at Discovery station 1654, 75° 43·6′ S., 176° 59·4′ E. on 25 January 1936.
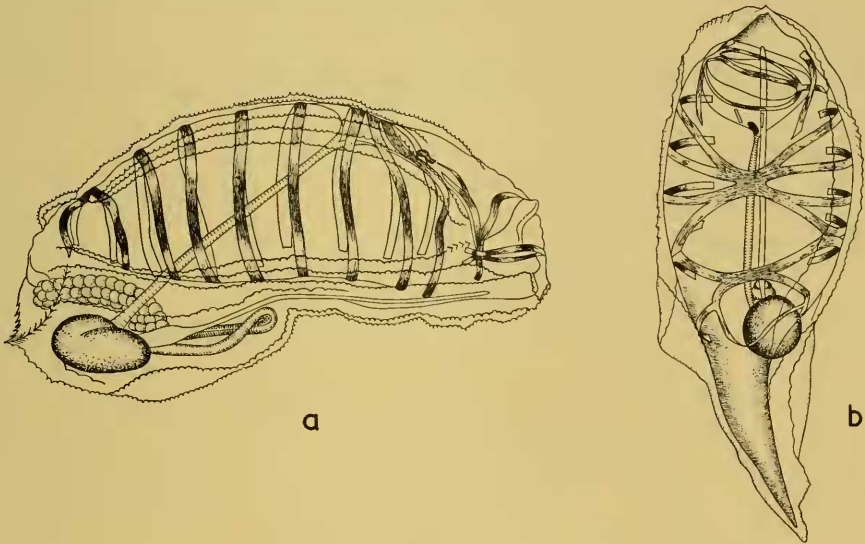
Text-fig. 2. *S. gerlachei* sp.nov. (*a*) Solitary form, lateral view. Length 27 mm. (*b*) Aggregate form, dorsal view. Length 17 mm. (From Van Beneden, 1913.) Note. The aggregate form shown here is atypical in lacking an anterior protuberance of the test; probably an artefact due to wear.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.1.

BODY PROPORTIONS. Total length 63 mm., body length 56 mm., nucleus length 11 mm.

MUSCLE-FIBRE NUMBER. 48 fibres in M. IV.

STOLON. Stolon with one fully differentiated block of buds consisting of 174 blastozooids, each 1 mm. long. Evidence that one block, at least, has already been released (see p. 25). Stolon extends forward to level of M. II–III.

ALLOTYPE. A specimen of the aggregate form 23 mm. long taken in a 1 m. net towed obliquely (N 100 B) from 109 m. to the surface at Discovery station 1296, 69° 06·6′ S., 131° 42·6′ W. on 1 March 1934.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.2.

BODY PROPORTIONS. Total length 34 mm., body length 23 mm., nucleus length 6 mm.

MUSCLE-FIBRE NUMBER. 127 fibres for the sum of M. I–VI counted along the right side.

EMBRYO. Single oozoid present.

PARATYPES. Five specimens of the solitary form taken in a 1 m. net (N 100 B) which fished between 440 and 190 m. at Discovery station 1257, 67° 52·4′ S., 129° 27·5′ W. on 11 January 1934.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.3.

Ten specimens of the aggregate form taken in a 1 m. net towed obliquely (N 100 B) from 109 m. to the surface at Discovery station 1296, 69° 06·6′ S., 131° 42·6′ W. on 1 March 1934.

REGISTRATION NUMBER. British Museum (Nat. Hist.). 1960. 10.18.4.

SOLITARY FORM (Text-fig. 2a)
(Based on the examination of sixty-seven specimens)

EXTERNAL APPEARANCE. Elongate. Similar to *S. thompsoni*.

TEST. Heavily serrated, firm. Pattern and number of serrated ridges identical with those in *S. thompsoni*, i.e. 'complex'.

BODY MUSCLES. Nine thin body muscles. M. I–III converge and join dorsally. M. IV–VII parallel. M. VIII–IX converge and join dorsally. Area of contact of the muscles that join dorsally is much smaller than in *S. thompsoni*.

MUSCLE FIBRES. Mean number 48·8 ± 1·8 for M. IV, based on 67 observations.

ALIMENTARY CANAL. Compact, oval nucleus.

STOLON. Similar to *S. thompsoni*.

LENGTH. Up to 75 mm.

AGGREGATE FORM (Text-fig. 2b)
(Based on the examination of fifty specimens)

EXTERNAL APPEARANCE. Body barrel shaped with conical anterior and posterior protuberances of the test. Similar to *S. thompsoni*.

TEST. Serrated. Disposition of the serrated ridges is the same as in *S. thompsoni*.

BODY MUSCLES. Six thin body muscles. M. I–IV and M. V–VI fuse dorsally to form two muscle groups. M. IV–V converge and join laterally.

MUSCLE FIBRES. Mean number 128·8 ± 3·2 for the total of M. I–VI, based on 50 specimens.

Table 1. *A summary of the features characterizing the four species of the 'fusiformis' group*

		Maximum body length (mm.)	External character of the test	Arrangement of the body muscles	Mean number of fibres	Width of muscles	Distribution
S. fusiformis	Aggregate	25	Smooth	M. IV–V laterally joined	51·8	—	North of S.T.C.*
	Solitary	45	Smooth	M. VIII–IX joined	29·4	—	
S. aspera	Aggregate	60	Serrated	M. IV–V separate	194·1	—	North of S.T.C.
	Solitary	95	Serrated (simple)†	M. VIII–IX parallel or nearly so	100·7	—	
S. thompsoni	Aggregate	60	Serrated	M. IV–V laterally joined	177·7	Broad 18·9:1‡	Middle latitudes of Southern ocean. Circumpolar
	Solitary	120	Serrated (complex)†	M. VIII–IX joined	93·2	Broad 21·2:1‡	Northern limit—S.T.C.
S. gerlachei	Aggregate	33	Serrated	M. IV–V laterally joined	128·8	Narrow 27·6:1‡	High latitudes of the Pacific sector of Southern Ocean
	Solitary	75	Serrated (complex)†	M. VIII–IX joined	48·8	Narrow 35·8:1‡	

* S.T.C. = subtropical convergence.   † For explanation of the terms 'simple' and 'complex' see pp. 10, 12.
‡ Ratio of body length : muscle width, see p. 23.

ALIMENTARY CANAL. Compact, oval nucleus.

EMBRYO. Single as in *S. thompsoni*.

DISTRIBUTION OF *S. GERLACHEI*. Confined to the high latitudes of the Pacific Sector of the Southern Ocean. Not circumpolar in its distribution.

KEY TO THE SPECIES

(The diagnostic characters are summarized in Table 1)

AGGREGATE

1. Test smooth; total fibre number 40–61 (mean 51·8).   *S. fusiformis*
   Test serrated; total fibre number more than 113.   2
2. Muscles IV and V approach but not in contact laterally.   *S. aspera*
   Muscles IV and V in contact laterally.   3
3. Muscle bands broad; total fibre number 140–235 (mean 177·7) (ratio of body length:muscle width, 18·9:1).
       S. thompsoni
   Muscle bands narrow; total fibre number 113–159 (mean 128·8) (ratio of body length:muscle width 27·6:1).
       S. gerlachei

SOLITARY

1. Test smooth; muscle fibres of M. IV 19–40 (mean 29·4).   *S. fusiformis*
   Test serrated; muscle fibres of M. IV 36–130.   2
2. Muscle bands VIII and IX parallel (or nearly so); test ridges 'simple' (see p. 10).   *S. aspera*
   Muscle band VIII and IX joined; test ridges 'complex' (see p. 12).   3
3. Muscle bands broad; fibres of M. IV 70–130 (mean 93·2) (ratio of body length:muscle width, 21·2:1).
       S. thompsoni
   Muscle bands narrow; fibres of M. IV 36–71 (mean 48·8) (ratio of body length:muscle width 35·8:1).
       S. gerlachei

MORPHOLOGICAL CHARACTERS OF TAXONOMIC IMPORTANCE

It is proposed in this section to deal with those aspects of the morphology that have proved to be of importance in understanding the taxonomy of *S. fusiformis* and its related species. For a detailed account of the morphology of the Salpidae in general reference should be made to the monographs of Ihle (1937–58). In the present study variations in the structure and arrangement of two features, the external test and the body musculature, have been found useful in distinguishing the different species, but it is not suggested that these same characters will necessarily be of equal significance in the other genera.

THE NUMBER OF FIBRES PER MUSCLE BAND

The muscle bands so characteristic of the Salpidae are composed of muscle fibres arranged parallel to each other and to the main axis of the muscle, and in many species the number per muscle can be counted using a low-power binocular microscope. Little significance has been attached to muscle-fibre number and only a few workers have considered it to be of taxonomic importance. Apstein (1906) distinguished between the aggregate forms of *S. mucronata* (= *T. democratica*) and *S. flagellifera* (= *T. longicauda*) on the basis of the number of fibres per muscle which was found to be characteristically different in the two species. Tokioka (1937) described from Japanese waters *Thalia democratica* var. *orientalis* using the form of the test and the high number of fibres per muscle to distinguish it from the solitary form of *T. democratica*. Sewell (1953) discusses *T. democratica* and its related forms in some detail and gives significantly different fibre counts for the type and for *T. democratica*

var. *orientalis*. He concludes (p. 28) that in the solitary form of *T. democratica* there is a definite tendency for the number of fibres per muscle to increase with age although his data (p. 32) show no such increase in the aggregate form nor in the solitary form of *T. democratica* f. *orientalis* (p. 36). Further data for specimens of both type and variety of *T. democratica* from waters of Algeria are given by Bernard (1958) which confirm the results of Tokioka (1937) and Sewell (1953). Berner (1954) has drawn attention to the marked difference in fibre number in *Ritteriella picteti* and *R. ambionensis*, two species which otherwise appear very similar.

Berrill (1950) has discussed fibre number in general and has shown (p. 592) that the aggregate form of a species not only has fewer muscle bands than the solitary form but that they are individually narrower owing mainly to differences in the number of constituent fibres and in part to differences in the diameter of individual fibres. His data show not only that the solitary form may have three to four times as many fibres per muscle as its respective aggregate form but, what is more important, that there may be a considerable difference in the counts for different species. The following are some of the data given for individual muscle bands:

S. fusiformis	solitary, 30–33 fibres	aggregate, 7 fibres
T. democratica	solitary, 10 fibres	aggregate, 3 fibres
S. maxima	solitary, 55–65 fibres	aggregate, 20 fibres

Furthermore, in every species examined by Berrill (p. 593) the number of fibre rudiments first discernible in the embryo or bud is also the final number to be found in the largest solitary or aggregate individual; in other words there is no increase in number with age.

In the course of checking Berrill's counts, specimens from the Southern Ocean, thought to be *S. fusiformis aspera*, were examined and it was immediately apparent that both aggregate and solitary forms had at least three times more fibres per muscle band than the number given for *S. fusiformis* by Berrill. From the subsequent examination of specimens from as wide a geographic range as possible it was obvious that on the basis of fibre count alone three of the four species within the *fusiformis* group could be distinguished.

The data for the aggregate and solitary forms of *S. fusiformis*, *S. aspera*, *S. thompsoni* and *S. gerlachei* are shown in Text-figs. 3 and 4, in which the fibre count for each specimen is plotted against its body length. Before discussing these results it is necessary to consider the treatment of the data, and the reasons for using the number of fibres in M. IV in the solitary form and the sum of the counts of M. I–VI in the aggregate form.

Specimens of the solitary form of all species, except *S. fusiformis*, in which all the nine body muscles were sufficiently well preserved to enable each to be counted, were comparatively rare. Thus while it was realized, as the data in Table 2 show, that the number of fibres varies slightly from muscle to muscle and even from side to side, it was decided to count the number of fibres in one muscle only of each specimen. Body muscle IV proved convenient for this purpose as it is easy to locate and counts were made on the dorsal surface as near to the middle line as possible. A further reason for using one muscle is that *S. thompsoni* has a very high fibre count, ranging from 70 to 130 fibres per muscle, which would make the counting of all nine muscles in each specimen unduly tedious and quite unnecessary for specific identification.

For the aggregate form total counts, that is the sum of the number of fibres in each body muscle (counted along the same side if possible), are used because, as the data in Table 2 show, there is considerable variation in fibre number from muscle to muscle. While such variation is insufficient to mask any difference based on single muscle counts between *S. fusiformis* and the other species, it is great enough to make the differentiation of *S. thompsoni* and *S. gerlachei* obscure.

In Text-fig. 3 *a* and *b* individual counts for both forms of *S. fusiformis* and *S. aspera* are compared while the mean values are given in Table 3. Compared to the rather limited data for *S. aspera* the fibre counts for *S. fusiformis* show relatively little scatter about the mean of 51·8±1·4 for the aggregate and 29·4±1·4 for the solitary form. It is also evident, for all species, but particularly in the case of *S. fusiformis*, that there is no increase in the number of fibres per muscle as the animal grows in size. The number of observations for *S. aspera*, particularly of the solitary form, are limited and so the means of 194·1 for aggregate and 100·7 for solitary forms must be considered as approximate. Even so there is no overlap between the counts for *S. fusiformis* and *S. aspera* and the difference between

Table 2. *Individual muscle-fibre counts in the solitary and aggregate forms of three of the four species showing (a) the variation in fibre number between muscles, (b) the variation in fibre number between the left and right sides of the same muscle in* Salpa fusiformis *and (c) the variation in the number of muscle fibres from species to species.* (S. aspera *is not included because counts of individual muscles are not available for the solitary form*)

	St.	Body length (mm.)		I	II	III	IV	V	VI	VII	VIII	IX	Total
							Body muscle						
						Solitary							
S. fusiformis	3097	40	Left	36	29	30	30	31	28	36	34	28	282
			Right	31	31	31	27	32	34	33	37	28	284
S. thompsoni	1392	35	Left	60	68	68	82	82	77	83	70	70	660
S. gerlachei	2226	65	Right	35	31	38	40	34	29	28	35	36	306
						Aggregate							
S. fusiformis	3097	22	Left	11	5	10	9	9	11	—	—	—	55
			Right	12	7	7	9	9	11	—	—	—	55
S. thompsoni	2020	20	Right	37	28	28	27	29	36	—	—	—	185
S. gerlachei	2226	17	Left	26	22	19	19	20	21	—	—	—	127

Table 3. *The variation in the mean number of muscle fibres in the four species, with the standard deviation and number of observations for each species. Standard deviations have not been given for* S. aspera *because of insufficient data for the solitary form*

	Mean number of muscle fibres	Standard deviation	Number of observations
	Solitary (M. IV)		
S. fusiformis	29·4	4·8	48
S. aspera	100·7	—	9
S. thompsoni	93·2	13·8	92
S. gerlachei	48·8	7·3	67
	Aggregate (M. I–VI)		
S. fusiformis	51·8	4·9	45
S. aspera	194·1	—	29
S. thompsoni	177·7	18·7	126
S. gerlachei	128·8	11·3	50

them as shown in Text-fig. 3 and from the data of Table 3 is most striking. Text-fig. 3 also illustrates the great difference in the maximum size attained in the two species, at least as represented by the specimens available, *S. aspera* at its maximum being two to three times larger than *S. fusiformis* at comparable stages of maturity.

Text-fig. 4 shows the data for *S. thompsoni* and *S. gerlachei*. Comparing Text-fig. 4 with Text-fig. 3 it will be seen that *S. fusiformis* in both its forms has fewer fibres per muscle than any of the other species, and does not attain the relatively large size of the other species. The data plotted in Text-fig. 4 for both forms of *S. thompsoni* and *S. gerlachei* show considerable scatter in the observations. Never-

theless, the data fall into two well-defined groups, one for *S. thompsoni* with a mean value of 177.7 ± 3.4 for the aggregate and 93.2 ± 2.8 for the solitary, and the other for *S. gerlachei*, with means of 128.8 ± 3.2 and 48.8 ± 1.8 for aggregate and solitary, respectively. The difference between the species is even more obvious from Text-fig. 5 based on the data of Table 4 which gives the percentage frequency of occurrence of the various muscle fibres for the two species, and, for comparison, the data for *S. fusiformis*. Text-fig. 5 shows that in the solitary form *S. thompsoni* and *S. gerlachei* are quite distinct.
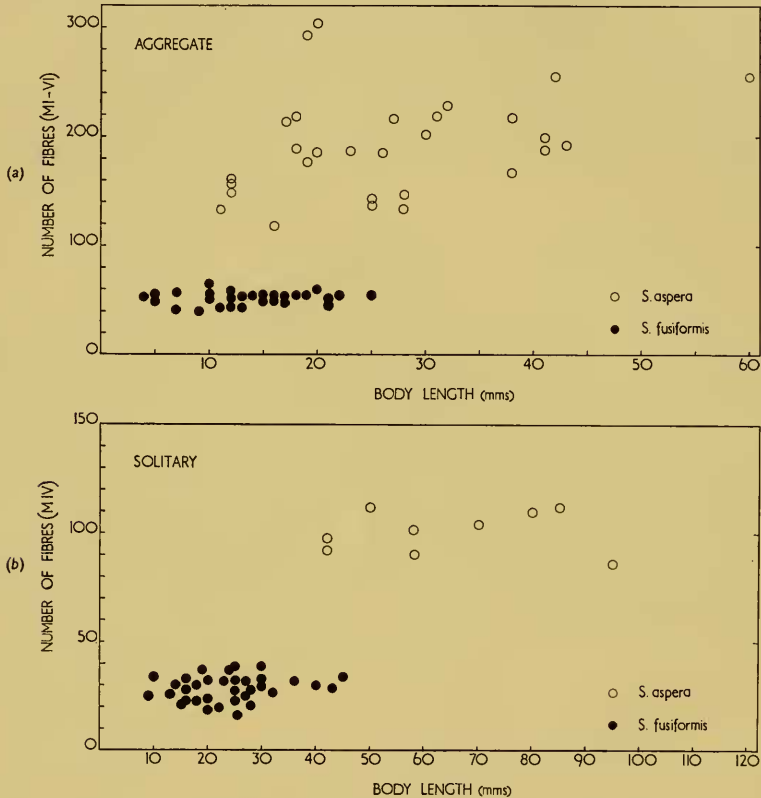
Text-fig. 3. Variation in the number of muscle fibres in *S. fusiformis* and *S. aspera*; (*a*) the aggregate form (M. I–VI, see text) and (*b*) the solitary form (M. IV), plotted against body length.

Although there is overlap between the data for the solitary forms of *S. gerlachei* and *S. fusiformis* there can be little confusion between them when other features (such as the character of the external test) are considered and particularly since they occur, as will be shown later, at the opposite ends of the range of distribution of this group of four species (see Text-fig. 6).

The data for the aggregate forms of *S. thompsoni* and *S. gerlachei* in Text-figs. 4*a* and 5 show that the difference between them is not so marked as it is in the solitary form. Nevertheless, two distinct groups can be seen with means of 177.7 and 128.8 for *S. thompsoni* and *S. gerlachei*, respectively, (Table 3). It will be noted both from Table 3 and Text-fig. 5 that *S. fusiformis* with a mean of 51.8 fibres for M. I–VI cannot be confused in its aggregate form with either *S. thompsoni*, *S. gerlachei* or *S. aspera*.
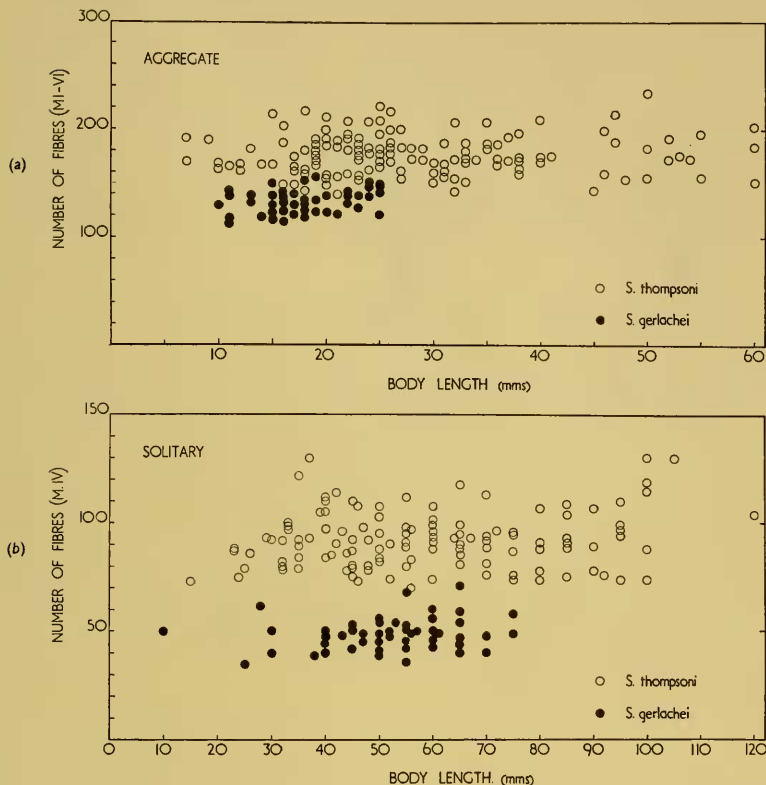
Text-fig. 4. Variation in the number of muscle fibres in *S. thompsoni* and *S. gerlachei*; (*a*) the aggregate form (M. I–VI) and (*b*) the solitary form (M. IV) plotted against body length.

Table 4. *The percentage frequency of occurrence of muscle fibre counts in the solitary and aggregate forms of* Salpa fusiformis, S. thompsoni *and* S. gerlachei; *based on the data plotted in Text-figs. 3 and 4.*

Fibre no. ...		10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120	120–130	130–140
						Solitary (M. IV)								
S. fusiformis	Number of specimens	2	26	24	1	—	—	—	—	—	—	—	—	—
	%	3·8	49·1	45·4	1·9	—	—	—	—	—	—	—	—	—
S. gerlachei	Number of specimens	—	—	5	40	23	3	2	—	—	—	—	—	—
	%	.	—	6·8	54·8	31·5	4·1	2·7	—	—	—	—	—	—
S. thompsoni	Number of specimens	—	—	—	—	—	—	25	36	47	13	10	1	3
	%	—	—	—	—	—	—	18·5	26·6	34·8	9·6	7·4	0·7	2·2

Fibre no. ...		40–50	50–60	60–70	110–120	120–130	130–140	140–150	150–160	160–170	170–180	180–190	190–200	200–210	210–220	220–230	230–240
							Aggregate (M. I–VI)										
S. fusiformis	Number of specimens	12	31	2	—	—	—	—	—	—	—	—	—	—	—	—	—
	%	26·7	69·0	4·4	—	—	—	—	—	—	—	—	—	—	—	—	—
S. gerlachei	Number of specimens	—	—	—	7	17	27	25	6	—	—	—	—	—	—	—	—
	%	—	—	—	8·5	20·7	32·9	30·5	7·3	—	—	—	—	—	—	—	—
S. thompsoni	Number of specimens	—	—	—	—	—	—	11	16	29	34	31	16	13	5	1	1
	%	—	—	—	—	—	—	7·0	10·2	18·5	21·6	19·7	10·2	8·3	3·2	0·6	0·6

3-2
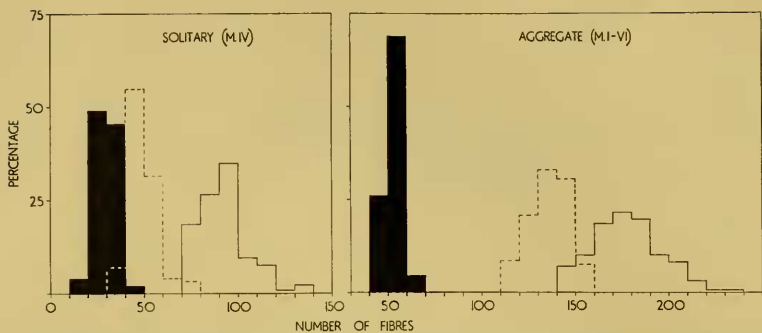
Text-fig. 5. The percentage frequency of occurrence of muscle-fibre counts in the aggregate and solitary forms of *S. fusiformis* (black solid), *S. thompsoni* (solid line) and *S. gerlachei* (broken line).
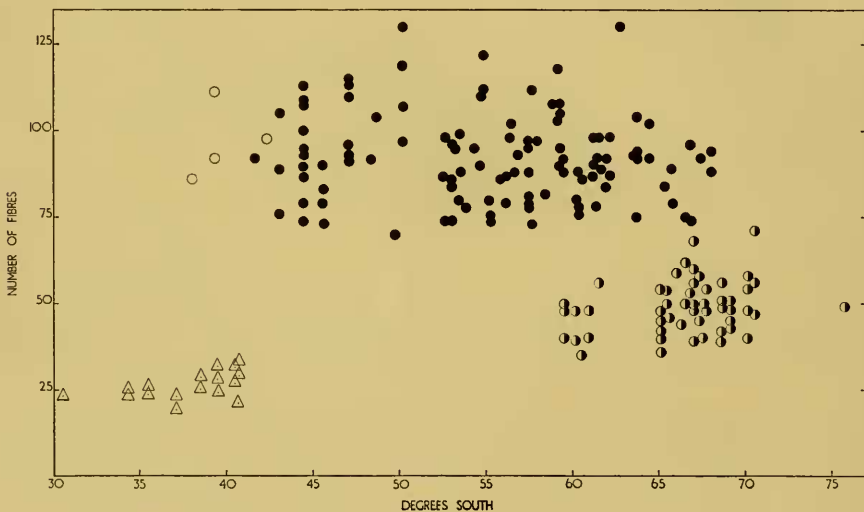
Text-fig. 6. Individual muscle-fibre counts of specimens of the solitary form of *S. fusiformis* (△), *S. aspera* (○), *S. thompsoni* (●) and *S. gerlachei* (◐) plotted according to the latitude of the station at which they were taken. Note: observations for *S. fusiformis* and *S. aspera* at stations north of 30° S. are not included.

The data for *S. aspera* are insufficient to show the percentage frequency of occurrence as has been done for the other species. However, when the data plotted in Text-fig. 3 are compared with those of Text-fig. 4 it is seen that in fibre number *S. aspera* lies roughly within the same range as *S. thompsoni*. It is thus impossible to distinguish these two species on the basis of their muscle-fibre number but it will be remembered (Table 1, pp. 14 and 15) that they can be distinguished in both aggregate and solitary form by differences in their muscle arrangement, and in addition, in the solitary form, by external differences in serrations of the test.

As mentioned above there is overlap between the fibre counts for some of the species, as, for instance, between the solitary forms of *S. fusiformis*, *S. thompsoni* and *S. gerlachei* (Text-fig. 5) and it might be argued that *S. gerlachei*, characterized by fewer muscle fibres and thinner muscles (see

p. 23) than *S. thompsoni* but otherwise identical in all other morphological features, represents an extreme of variation. On this assumption one might expect there to be some sort of gradation in muscle fibre number between the limits of the animal's distribution. In Text-fig. 6 the data (for stations south of 30° latitude) for the solitary form of each species have been plotted against the latitude of the station at which they were taken, and it is apparent that no such gradient exists in the character of muscle-fibre number from north to south, the change from 'many fibres' to 'few fibres' being particularly abrupt. It will be noted that *S. aspera* on rather limited data has similar counts to *S. thompsoni* and so, as mentioned above, this character cannot be used to distinguish these two species.

The Arrangement of the Body Muscles

Unlike the external character of the test great reliance has been placed by many previous workers on muscle arrangement for differentiating salp species, and Streiff (1908) and others have given detailed accounts of the body, atrial and oral muscles of most species. While the arrangement of the atrial and oral muscles is both complex and difficult to study, the body muscles are relatively simple and easy to see, so making them useful as taxonomic characters particularly as their arrangement within a species is more or less constant. Sewell (1926, p. 67) has remarked that large variations do occur both with regard to the number of muscle bands and the connexions between them, and warns that the muscles are delicate and so their arrangement can be altered by rough handling. As an example Thompson (1948, Pl. 73, fig. 3) shows the variation that can occur in the connexions of the body musculature of the solitary form of *S. cylindrica*. Nevertheless, in most species muscle arrangement may be combined with other characters, and it remains one of the most useful taxonomic features (Yount, 1954).

In three of the four species described, *S. fusiformis*, *S. thompsoni* and *S. gerlachei*, there is the same basic arrangement of body muscles. In the aggregate form there are six dorsal body muscles which curve laterally to the ventral surface where they are interrupted. The six muscles are disposed in two groups with dorsal fusion of M. I–IV and M. V–VI; and lateral fusion of M. IV and V. The solitary form has nine body muscles which like the aggregate are interrupted ventrally. There is dorsal fusion of M. I–III and M. VIII–IX, while M. IV–VII are parallel to each other.

S. aspera (Pl. I) has the same basic muscle arrangement as that just described except that in the aggregate form (Pl. I *b*) M. IV–V converge but do not join laterally and in the solitary form (Pl. I *a*, *c*) M. VIII–IX do not join but like M. IV–VII are parallel or nearly so.

It will be shown in the section on distribution that *S. fusiformis* and *S. aspera* are sympatric and so on occasions are taken together in the same net sample. From the foregoing it will be realized that setting aside other differences such as test character and muscle-fibre number there is no striking difference between *S. fusiformis* and *S. aspera*, except in the arrangement of body muscles in the solitary form, and as the two species can occur together this has contributed to the confusion, particularly with regard to the aggregate form of the two species, described in the historical section. Herdman (1888), for example, differentiated the solitary form of *S. echinata* on the basis of serrated test and M. VIII–IX being parallel, but failed to associate it with specimens of the aggregate form in his collection in which M. IV–V did not join laterally, regarding the latter as variations of *S. runcinata* (= *S. fusiformis*). There has in fact been little significance attached to the lateral separation of M. IV–V in the aggregate form, such separation being regarded as a mere variant (Herdman, 1888) or a character associated with old age (Ritter, 1905): the latter in spite of Apstein's illustration (1894 *b*, Pl. II, fig. 14) of a small blastozooid (4 mm. long) with M. IV–V laterally separate taken from the stolon of a solitary form in which M. VIII–IX were parallel.

There seems little doubt, however, in view of the evidence presented in this paper, that previous records of the 'asperate' form of *S. fusiformis* from temperate or tropic seas are of the same species as the one that I have renamed *S. aspera*, because in every paper in which such serrated specimens of the aggregate form are figured they are shown with a muscle plan in which M. IV–V do not join laterally (for example, Herdman, 1888, Pl. VI, fig. 6; Apstein, 1906, Pl. XXVI, fig. 6; Yount, 1954, fig. 12*b*). Furthermore, where a serrated solitary form is figured it is shown with M. VIII–IX parallel or nearly so (Herdman, 1888, Pl. V, figs. 1–4; Ritter, 1905, fig. 14; Yount, 1954, fig. 11*a*).

There are, however, in the literature, three notable exceptions. Herdman (1888, Pl. VI, fig. 5) figures a serrated specimen of the aggregate form in which M. IV–V join laterally, Apstein (1906, Pl. XXVI, fig. 6) shows a serrated solitary form with M. VIII–IX joined medio-dorsally, while Metcalf (1918, fig. 80) figures a different view of what appears to be a similar specimen to that of Apstein. Herdman's and Apstein's figures, however, are of specimens from the Antarctic and so from the data presented in this paper conform not to *S. aspera* but to *S. thompsoni*. The figure in Metcalf's paper is not original, being based on that of Ritter (1905, fig. 14) and it seems not unlikely that in it are combined the characters of test given by Ritter (for Californian specimens) with the plan of muscle arrangement given by Apstein (1906, Pl. XXVI, fig. 6) for an antarctic specimen. Such an association of characters has not appeared in any of the specimens examined in this study.

THE EXTERNAL CHARACTER OF THE TEST

The presence of serration or denticulations on the external surface of the test of some species of salps has been noted by many workers and has in some cases been used as a character for the separation of new species, subspecies or variants; for example, *T. democratica* var. *orientalis* Tokioka (1937), *S. maxima* var. *tuberculata* (Metcalf, 1918) and *S. fusiformis aspera* (Ihle, 1911). Sewell (1926, 1953) discusses the occurrence of such denticulations at some length both in the Salpida and Pyrosomida and concludes that, owing to the complete intergradation between smooth and serrated forms, they are of little importance as characters for systematic differentiation, and attributes the variability of this feature to the great degree of plasticity inherent in the Salpida (see also Metcalf, 1918, p. 5). The evidence of Yount (1958) would seem to confirm this view and in the case of *S. fusiformis* serrated and smooth forms are listed as the one species. The results of the present study are contrary to the conclusions of Sewell and Yount, at least in so far as they relate to *S. fusiformis* and its related species. It was noted at the outset without the use of any special technique that two basic test forms could be recognized, one smooth and the other serrated and while this character alone does not allow all the four species to be distinguished it can be combined with other features and used for their identification.

Detailed examination of the external surface of the test shows, as Stiasny (1926) has described, the presence of areas of thickening which give it a ridged appearance. In species with serrated tests the denticulations occur along these ridges, the arrangement of which in the solitary form in particular follows a definite pattern, the finer detail of which is easily visible when the test is stained with toluidine blue or methylene blue (see p. 5). As the serrations are a feature of the external surface of the test they are subject to wear, and with increased age tend to become smooth, particularly in the aggregate form. Staining, however, allows the remnants of the serrated areas to be detected in specimens which to the casual observer might appear smooth.

The aggregate form of *S. fusiformis* (p. 9) has a smooth test devoid of any serrations and so can be distinguished from the three serrated species. It is not possible, however, in the aggregate form to differentiate the serrated species from each other on the basis of the external test, since the pattern of arrangement is less definite and possibly more subject to variation. Of the species, the two which

occur in the Southern Ocean, *S. thompsoni* and *S. gerlachei*, are typically more heavily serrated than *S. aspera*, having the arrangement of serrated ridges shown in Pl. II *b* and Text-fig. 2 *b*. In the aggregate form of *S. aspera* (Pl. I *b*) the serrations appear to be irregularly scattered over the test with a tendency to be well developed on the anterior and posterior processes.

The solitary, like the aggregate, form of *S. fusiformis* has a smooth test with a pattern of thickened ridges similar to that of *S. aspera* (Pl. I *c*), except of course for the absence of serrations on all ridges, and is identical with the descriptions given by Herdman (1888) and Ritter (1905). A basically similar arrangement of serrated ridges is found in *S. thompsoni* (Pl. II *a, c*) and *S. gerlachei* (Text-fig. 2 *a*) except for a more elaborate pattern on the dorsal surface where the secondary ridges, and particularly the presence of a medio-dorsal ridge (ridge no. 9 in Pl. II *c*), distinguish these two species from *S. aspera*. It is thus possible, using the external character of the test of the solitary form, to distinguish between *S. fusiformis*, *S. aspera* and *S. thompsoni* or *S. gerlachei*. Other characters, however, must be used to distinguish between *S. thompsoni* and *S. gerlachei*.

It has often been suggested that serrations are associated with age. Both Ritter (1905) and Farran (1906), for example, conclude that in *S. fusiformis aspera* serrations occur in the larger, older specimens. Apstein (1894 *b*), on the other hand, describes serrations in the smaller, younger specimens of *Thalia democratica*. Sewell (1953), however, considers that 'such a condition of the test may occur at any age up to mid-life, after which they tend to be eroded away'. In the present study it has been possible to examine specimens of at least one serrated species, *S. thompsoni*, in every stage of its development and so it is possible to make some generalizations about the occurrence of denticulations.

Very young aggregates (3–4 mm. long) while still part of the stolon of the solitary form have a thin poorly developed test which shows no external sign of serrations. The smallest released free-living aggregates, 5 mm. in length, however, have a well-developed test characteristically serrated. It thus seems reasonable to infer that when a block or chain of aggregates is released from the solitary form there is very rapid test development which in *S. thompsoni* and *S. gerlachei* and probably also *S. aspera* is accompanied by the formation of serrated ridges. In larger, older specimens as Sewell (1953) described, the denticulations tend to wear away but in the largest specimens of the aggregate form of each serrated species examined some serrations were quite obvious.

The solitary form, while still an embryo within the oozoid (aggregate), has a poorly developed test with no indication of denticulations, even though it may, before its release, attain a size of 9–10 mm., having all the morphological features of the adult, including a rudimentary stolon, already developed within it. In free-living solitary individuals in the 10–15 mm. size range the characteristic pattern of serrated ridges can be seen, so that as with the aggregate form one can infer that serrations develop very rapidly on the release of the embryo. Larger specimens often show evidence of a worn test, but in all cases examined it was possible to see the pattern of serrations and so distinguish, for example, *S. aspera* from *S. thompsoni* or *S. gerlachei*.

The Width of the Body Muscles in *Salpa thompsoni* and *S. gerlachei*

It will be realized from the previous sections that the only precise taxonomic difference between *S. thompsoni* and *S. gerlachei* is in the number of fibres per muscle band. Other characters, however, which are less easy to define in precise terms, make it possible readily to distinguish these two species. One such character is the difference in relative width of the muscle bands in specimens of approximately the same size.

Contained in the preliminary analysis of the samples collected by R.R.S. 'Discovery II' in the Southern Ocean are reports of the occurrence of specimens of '*S. fusiformis aspera*' with 'narrow or thin muscles', such comments being restricted to those samples taken in high latitude Pacific waters.

In this respect it is interesting to note that Herdman (1910, p. 21) records a specimen of the solitary form taken at 67° 5′ S., 179° 30′ E. which had muscle bands narrower than those of his other specimens. Subsequent examination of the Discovery material has shown such specimens to be *S. gerlachei* and it thus seemed worthwhile to measure the width of the muscles in *S. thompsoni* and *S. gerlachei* and see whether there was any significant difference between them. For this purpose a micrometer eyepiece was used and a measurement was made of body muscle IV in both the aggregate and solitary form of each species. The data are shown in Text-figs. 7 and 8. It must be remembered that muscle width, unlike the muscle-fibre number, which remains constant throughout the life of the animal,
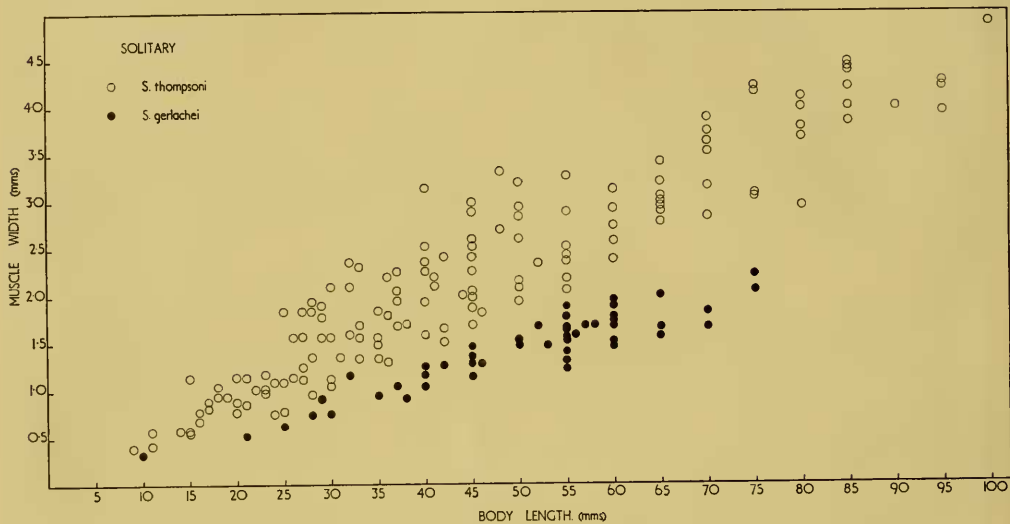
Text-fig. 7. Variation in the width of M. IV with body length in the solitary forms of *S. thompsoni* and *S. gerlachei*.
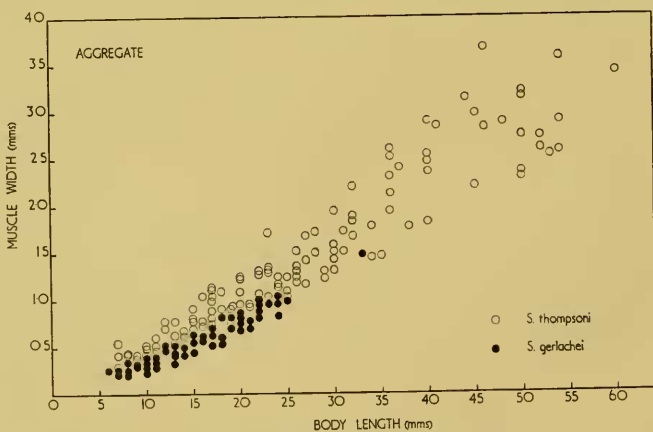
Text-fig. 8. Variation in the width of M. IV with body length in the aggregate forms of *S. thompsoni* and *S. gerlachei*.

increases as the animal grows in size. As previously mentioned (p. 5) body length cannot be measured in the larger specimens with great accuracy and this no doubt contributes to the considerable scatter of the data plotted in Text-figs. 7 and 8. Even allowing for this scatter, particularly in the data for *S. thompsoni*, it is obvious from Text-fig. 7 that in the solitary form *S. gerlachei* has much thinner muscle bands than *S. thompsoni*.

Text-fig. 8, in which data for the aggregate form of each of the two species has been plotted, show that there is again differentiation between *S. thompsoni* with wide muscle bands and *S. gerlachei* with thin muscle bands, although the difference is not so marked as it is in the solitary form (see Text-fig. 7). From Text-fig. 8 it is obvious that there is considerable scatter in the observations which makes muscle width in the aggregate form a character of doubtful value for differentiating between the two species, even though the data for *S. gerlachei* consistently fall in the lower part of the graph.

Table 5. *The variation in muscle width in* Salpa thompsoni *and* S. gerlachei *expressed as the ratio body length: muscle width, together with the number of observations.*

	Mean ratio of body length: muscle width	Number of observations
	Solitary	
S. thompsoni	21·2:1	57
S. gerlachei	35·8:1	53
	Aggregate	
S. thompsoni	18·9:1	33
S. gerlachei	27·6:1	57

The results plotted in Text-figs. 7 and 8 may be expressed as numerical ratios of body length and muscle width (Table 5) when it is seen that there are significant differences between the ratios for the solitary forms of the two species. As mentioned above, owing to variability in the data, the ratios for the aggregate form cannot be considered to be reliable.

The Development of the Stolon in *Salpa thompsoni* and *S. gerlachei*

A consideration of stolon development and budding in the solitary form is outside the scope of this paper and will be described in a later work. There are, however, certain differences between *S. thompsoni* and *S. gerlachei*, both in the size of the chains of buds and the size of the parent solitary individual at the time of release which, with the morphological differences already described, lend support to the view that they are in fact valid species. These differences will be discussed briefly here.

In the stolon of a mature solitary individual, that is, one in which a chain of aggregates (blastozooids) is about to be released, three zones or blocks of bud formation can be distinguished, the distal two being fully differentiated into a number of segments or buds which can be counted. When the oldest distal block, which I shall refer to as block 1, reaches a certain size it is shed in its entirety through a hole in the test so leaving a section of empty tube in the test. In the species to be described the hole formed by the release of a block is sealed off by a tissue 'strand' of granular appearance which remains as evidence that one block of buds at least has been released. The section of empty tube in the test which was occupied by block 1 is quickly filled by the growth of block 2 which thus becomes the distal block. It is probable that this block is subsequently released and replaced by block 3 which may in turn on its release be replaced by another block. It will be realized from the foregoing that while it is possible, from the absence of a strand of granular tissue in the test, to deduce with certainty that no blocks have been released it is not possible to say, in the presence of a strand, whether the

distal block is block 2, 3 or 4. Nevertheless, the presence or absence of this granular strand is a valuable indication of the relative maturity of the solitary form. The smallest specimens in which it occurs provide evidence of the minimum body size at which chains of buds can be released, while the number of buds present in the distal block is an indication of the potential number of aggregates that can be released by one solitary individual at any one time.

Data have been accumulated from the examination of 287 specimens of *S. thompsoni* and 57 specimens of *S. gerlachei* and the results are given in Table 6 and Text-fig. 9. Table 6 compares the mean number of buds in block 1 (no strand) and block 2 (strand) with the body size of the specimen on which the
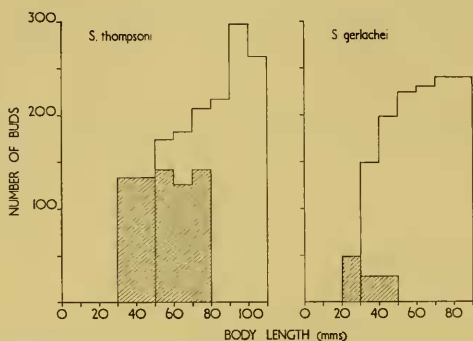
Text-fig. 9. Budding in *S. thompsoni* and *S. gerlachi*. The mean number of buds produced in the first (shaded) and second (unshaded) blocks of *S. thompsoni* and *S. gerlachei* plotted against body length. Full explanation in text.

Table 6. *The relationship between body length and budding in* Salpa gerlachei *and* S. thompsoni. *For full explanation see text.*

Size group (mm.) ...		20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	Total no. of specimens
				S. gerlachei							
Block 1	Mean number of buds	49·0	27·0	28·0	—	—	—	—	—	—	—
	Number obsv.	2	2	2	—	—	—	—	—	—	6
Block 2	Mean number of buds	—	149·2	198·6	223·6	229·0	240·0	240·0	—	—	—
	Number obsv.	—	5	20	14	8	3	1	—	—	51
				S. thompsoni							
Block 1	Mean number of buds	—	133·2	133·6	142·2	126·0	141·6	—	—	—	—
	Number obsv.	—	17	57	65	53	13	—	—	—	205
Block 2	Mean number of buds	—	—	—	174·6	181·2	207·2	217·0	297·2	262·0	—
	Number obsv.	—	—	—	3	18	31	19	7	4	82

Mean number of buds in block 1. *S. gerlachei*: 38·0 (6 obs.).
Mean number of buds in block 1. *S. thompsoni*: 134·8 (205 obs.).

count was made, the data being treated in size groups of 10 mm. interval. The data for *S. gerlachei* are limited to specimens taken in a period from November to February and to eliminate seasonal differences, if any, the *S. thompsoni* specimens are also from stations in these months. In plotting the data in Text-fig. 9 it has been assumed that the distal block in those specimens with a strand is in fact block 2; it is obvious from the results that this is probably not a valid assumption, particularly for *S. thompsoni*; nevertheless, it in no way invalidates the argument that follows.

The data in Table 6 and Text-fig. 9 show that there are a number of obvious differences between *S. thompsoni* and *S. gerlachei* both in the number of buds initially produced—block 1—and in the size of the solitary form when this block is released.

MORPHOLOGICAL CHARACTERS OF TAXONOMIC IMPORTANCE

In *S. thompsoni* the first fully differentiated block of buds occurs in the 30–40 mm. size range and may be released, as indicated by the presence of a strand, at 50–60 mm. although release may not occur until the animal is 70–80 mm. long. The number of buds in block 1 is remarkably constant in each size group with a mean, based on 205 specimens, of 134·8 buds. It will be noted that subsequent blocks, as shown by the data from specimens with strands (block 2, in the figure) have a significantly greater number of buds than block 1, which suggests that the animal's capacity to produce buds increases as it grows. This view is further supported by the very high mean values of 297·2 and 262·0 buds per block for animals in the 90–100 mm. and 100–110 mm. size range; these blocks, as mentioned above, probably being blocks 3 or 4—in other words those produced subsequently to the release of block 2.

In *S. gerlachei*, block 1 is fully segmented at a body size of 20–30 mm. compared with 30–40 mm. in *S. thompsoni*, while it is released at a size of 30–40 mm. compared with 50–60 mm. in the other species. Block 1 in *S. gerlachei* has strikingly fewer buds than *S. thompsoni* with an average of 38·0 buds per block, although it should be noted that this is based on only six specimens. Subsequent blocks have about the same mean number of buds as in specimens of *S. thompsoni* of comparable body length.

The data thus show that compared with *S. thompsoni*, *S. gerlachei* produces initially in block 1 significantly fewer buds which are released when the solitary form is relatively much smaller. These differences in asexual development might be attributed to environmental change, the specimens being geographical races of the same species. In view, however, of the differences in morphological character that are apparent in both aggregate and solitary forms it is assumed that they are specific differences.
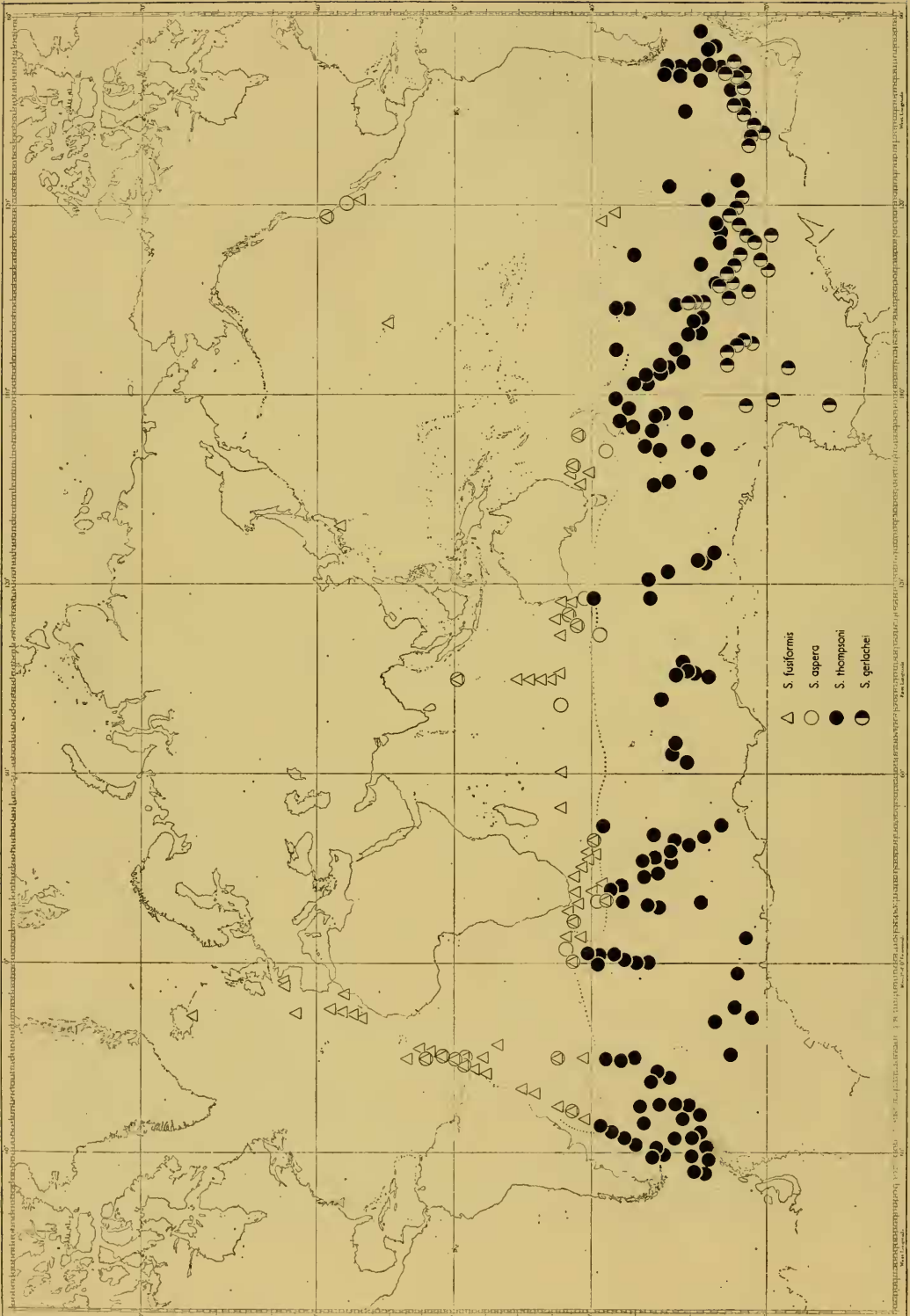
DISTRIBUTION

Any consideration of the distribution of the four species described in this paper is limited by the geographical range of the stations from which samples were available for study. As mentioned previously (p. 5) most of the stations are from the Southern Ocean and only a relatively few lines of observations extend north of the subtropical convergence. These latter stations have been supplemented by material made available by other workers which, however, as a consequence are rather scattered in geographical location. Nevertheless, in spite of the relative paucity of data from areas other than the Southern Ocean, an attempt has been made in Text-fig. 10 to show the occurrence of the four species on a world chart using all the stations from which material has been personally examined.

Text-fig. 10 shows the positions at which the various species have been recorded, each species being indicated by a different symbol. Also indicated in the figure is the mean position of the subtropical convergence based on Deacon (1937). With regard to this convergence it should be remembered that although as a physical-chemical feature it is well defined it is more variable in position than the antarctic convergence; and, furthermore, its position in some areas, particularly the eastern Pacific, is largely conjectural.

From Text-fig. 10 it is obvious that the region of the subtropical convergence represents a faunistic boundary, at which two of the species, *S. fusiformis* and *S. aspera*, reach the southern limit of their distribution. For *S. thompsoni* it is the northern limit to its range. Records of these species either north or south of what is apparently their normal range do occur, but in Text-fig. 10 the mean position of the subtropical convergence is shown and if its contemporary position could have been plotted for each crossing by a line of stations its appearance as a boundary would be even more clearly defined.

Text-fig. 10 shows that both *S. fusiformis* and *S. aspera* have been taken north of the subtropical convergence in Pacific, Atlantic and Indian Oceans. It is not possible from the data available to define the northern limit to the distribution of either species, although in the present material, *S. fusiformis* has been recorded as far north as 63° 51′ N., 16° 20′ W. while *S. aspera* has been recorded at 37° 24′ N.

Text-fig. 10. The distribution of *S. fusiformis*, *S. aspera*, *S. thompsoni* and *S. gerlachei* based on all available material actually examined. The approximate mean position of the subtropical convergence is shown as a dotted line about 40° S.

123° 23′ W. It will be seen from Text-fig. 10 that *S. thompsoni* is typical of other Southern Ocean plankton in being circumpolar in its distribution (Baker, 1954). *S. gerlachei*, on the other hand, is restricted to the Pacific, occurring with one exception in a sector between 65° S. and the ice edge roughly between 175° E. and 80° W. The distribution of this species compared to other antarctic species is thus remarkable in not being circumpolar. An apparent anomaly in distribution occurs in the region of 150° W. where there are a number of records of *S. gerlachei* to the north of 65° S. Specimens of the solitary form were taken in 1951 at stations 2743 and 2744, and as an independent check, I was able to examine specimens taken on the 1949 Brategg Expedition where *S. gerlachei* occurred at two stations which were nearly coincident in position to the 'Discovery' stations. Hydrological observations in this area (Deacon, 1937, p. 31; Midttun and Natvig, 1957) suggest that there may be a northerly outflow of surface water from the Ross Sea similar to that of the Weddell Sea current in the Atlantic. Such a current system might account for the northward extension to the animals' distribution that is a feature of this area. With the exception of these observations, *S. gerlachei* ranges from the ice edge to about 65° S. and so occurs principally in an area of the West Wind Drift but possibly extending in the south into the East Wind Drift. How this species has evolved and is able to maintain itself in this area is not clear, since no known hydrological feature appears to serve as a boundary between its distribution and that of *S. thompsoni*. Waters with the same characteristics of temperature and salinity occur in other sectors of the Southern Ocean and yet *S. gerlachei* occurs only in the Pacific. It is also remarkable that *S. gerlachei* is not taken either in the Drake Passage or in the Bransfield Strait where there is interchange of water between the Pacific and the Atlantic (Deacon, 1937). This area particularly the Bransfield Strait is in fact frequently rich in salps, but at all the stations from which specimens have been examined, only *S. thompsoni* occurred.

With regard to the boundary between *S. thompsoni* and *S. gerlachei* it will be remembered (Text-fig. 6, p. 20) that the change in fibre count from one species to the other is abrupt, particularly when it is realized that in Text-fig. 6 the occurrences of *S. thompsoni* at positions south of 65° are without exception from sectors other than the Pacific. Mixing of the two species is of course possible and at station 1295 specimens of the solitary form of both species were taken in the same haul. They were, however, easily recognized using the characters described and presumably such occurrences can be attributed to localized water mixing.

While a consideration of the quantitative distribution of *S. thompsoni* and *S. gerlachei* is outside the scope of this present paper, and will be described later, it is worth noting that both species are taken at certain times of the year in great numbers as, for example, at station 1261 where 66,000 *S. gerlachei* were estimated to have been taken in a 20 min. (N 100 B) haul which compares with the richest hauls of *S. thompsoni* taken in more northerly waters.

SUMMARY

1. Within the 'fusiformis group' there has been a confusion of four species. Three of these have hitherto been variously known as *Salpa fusiformis aspera* to distinguish them from the type *S. fusiformis* Cuvier.

2. Using a complex of morphological characters which includes the number of fibres per muscle band, the arrangement of the body muscles, and the external character of the test the four species can be identified. They are *S. fusiformis* Cuvier, *S. aspera* Chamisso, *S. thompsoni* sp.nov., and *S. gerlachei* sp.nov.

3. Additional evidence based on variations in muscle width and stolon development supports the view that *S. gerlachei* should be distinguished from *S. thompsoni* and regarded as a separate species.

4. The southern limit to the range of distribution of both *S. fusiformis* and *S. aspera* is the subtropical convergence. The data do not allow the northern limit to be defined.

5. *S. thompsoni* has its northern limit of distribution at the subtropical convergence. It occurs in subantarctic and antarctic waters and is circumpolar in distribution.

6. *S. gerlachei* is an antarctic species restricted to high latitude waters of the Pacific sector and is remarkable in not having a circumpolar distribution.

REFERENCES

APSTEIN, C., 1894a. *Die Salpen der Berliner Zoologischen Sammlung*. Archiv. Naturgesch. Jahrg. 60, Bd. 1, pp. 41–54.

—— 1894b. *Die Thaliacen der Plankton-Expedition*. Ergeb. der Plankton-Exp. der Humboldt-Stiftung. Bd. II.

—— 1901. 'Salpidae, Salpen'. Nordisches Plankton, vol. 1. Kiel and Leipzig.

—— 1906. *Salpen der deutschen Tiefsee Expedition*. Wiss. Ergebn. Valdivia, vol. XII. Jena.

—— 1908. *Die Salpen der deutschen Südpolar Expedition*. Dtsch. Südpol. Exped. vol. IX. Berlin.

BAKER, A. DE C., 1954. *The circumpolar continuity of antarctic plankton species*. Discovery Rep. vol. XXVII, pp. 201–18.

—— 1959. *Distribution and Life History of* Euphausia triacantha *Holt and Tattersall*. Discovery Rep. vol. XXIX, pp. 309–40.

BENEDEN, E. VAN and M. DE SELYS-LONGCHAMPS, 1913. *Tuniciers. Caducichordata (Ascidiaces et Thaliaces)*. Expedition Belgica, 1897–99, Zool. III, pp. 3–122.

BERNARD, M., 1958. *Systématique et Distribution Saisonnière des Tuniciers Pélagiques d'Alger*. Rapports et Procès-Verbaux des Réunions, vol. XIV (Nouvelle série), pp. 211–31.

BERNER, LEO., 1954. *On the previously undescribed aggregate form of the Pelagic tunicate* Ritteriella picteti (Apstein) 1904. Pacific Sci. vol. VIII, no. 2, pp. 121–4.

BERRILL, N. J., 1950. *Budding and development in* Salpa. J. Morph. 87, pp. 553–606, 16 figs.

BOMFORD, T. K., 1913. *Some salps taken by R.I.M.S.S. 'Investigator' in the Bay of Bengal and Andaman Sea*. Rec. Ind. Mus. vol. IX, Miscellanea, p. 243, part IV, no. 16. Calcutta.

BROOKS, W. K., 1893. *The genus* Salpa. *With a supplementary paper by Maynard M. Metcalf*. Johns Hopkins Univ., Mem. II, pp. 1–396, pls. I–LVII.

CHAMISSO, A-VON, 1819. De Animalibus quisbusdam e classe Vermium Linnaeana. 1815–1818. Fasc. 1. De Salpa, pp. 1–24, pl. 1. Berolini.

CUVIER, G., 1804. *Mémoire sur les Thalides et sur les Biphores*. Ann. Mus. Hist. Nat., An. XII, Tome 4, pp. 360–82, pl. 68.

DAVID, P. M., 1955. *The distribution of* Sagitta gazellae *Ritter-Zahony*. Discovery Rep. vol. XXVII, pp. 235–78.

—— 1958. *The distribution of the Chaetognatha of the Southern Ocean*. 'Discovery' Rep. vol. XXIX, pp. 199–228.

DEACON, G. E. R., 1937. *The hydrology of the Southern Ocean*. 'Discovery' Rep. vol. XV, pp. 1–124.

FAGETTI, E., 1959. *Salpas Collectadas Frente A Las Costas Central Y Norte De Chile*. Rev. Biol. mar., Valparaiso, vol. IX, nos. 1–3, pp. 201–8, pl. VII.

FARRAN, G. P., 1906. *On the distribution of the Thaliacea and Pyrosoma in Irish waters*. Fish. Ireland Sci. Invest. 1906. Pt. II, App. 1. Dublin.

FORSKÅL, PETRUS, 1775. Descriptiones Animalium Avium, Amphibiorum, Piscium, Insectorum, Vermium; quae in itinere orientali observavit, pp. 112–17 (Salpa).

FRASER, J. H., 1959. *Plankton investigations from Aberdeen in* 1957. Ann. biol., Copenhague, vol. XIV (1957), pp. 29–30.

HARDY, A. C. and GUNTHER, E. R., 1935. *The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927*. Discovery Rep. vol. XI, pp. 1–456.

HERDMAN, W. A., 1888. *Report on the Tunicata collected during the voyage of H.M.S. 'Challenger' during the years 1873–76*. Part III. 'Challenger' Reports, Zoology, vol. XXVII, pp. 1–163.

—— 1910. *Tunicata*. Nat. Antarctic ('Discovery') Exped. 1901–4. Nat. Hist. vol. V, pp. 1–26.

IHLE, J. E. W., 1910. *Die Thaliacean der Siboga Expedition*. Siboga Expeditie, Monograph 56d. Leiden.

—— 1911. *Über die Nomenklatur der Salpen*. Zool. Anz. vol. XXXVIII, pp. 585–9. Leipzig.

—— 1912. *Desmomyaria*. Das Tierreich, vol. XXXII. Berlin.

—— 1935. *Desmomyaria*. Handb. Zool. (Kuckenthal), Bd. V, 2.

—— 1937–58. *Salpidae*. Bronn's Klassen. Band 3, Suppl. Tunikaten, Abt. 2, Buch 2, Lief. 2, 3, 4; pp. 69–401.

ISAACS, JOHN D. and LEWIS, W. KIDD, 1953. *Isaacs–Kidd midwater trawl*. Scripps Institution of Oceanography. S.I.O. Ref., 53–3, pp. 1–18.

KEMP, S., HARDY, A. C. and MACKINTOSH, N. A., 1929. *The 'Discovery' investigations, objects, equipment and methods*. Discovery Rep. vol. I, pp. 141–232.

KROHN, A., 1846. *Observations sur le génération et le développement des Biphores* (Salpa). Ann. Sci. nat., ser. 3 (Zool.), vol. VI, pp. 110–31.

MACKINTOSH, N. A., 1934 *Distribution of the macroplankton in the Atlantic sector of the Antarctic*. Discovery Rep. vol. IX, pp. 65–160.

METCALF, M. M., 1918. *The Salpidaea: a taxonomic study.* Bull. U.S. Nat. Mus. no. 100, vol. II, part 2, pp. 5–193, pls. I–XIV.

MEYEN, F. J. F., 1832. *Beiträge zur Zoologie, gesammelt auf einer Reise um die Erde.* Nova Acta Leop. Carol., vol. XVI, pp. 363–422.

MICHAEL, ELLIS L., 1918. *Differentials in behaviour of the two generations of* Salpa democratica *relative to the temperature of the sea.* Univ. Calif. Pub. Zool. vol. XVIII, no. 12, pp. 239–98, pls. 9–11, 1 fig. in text.

MICHAELSON, W., 1915. *Tunicata.* Beitr. Meeresfauna Westafr. vol. I, p. 319. Hamburg.

MIDTTUN, LARS and NATVIG, JOHAN, 1957. *Pacific Antarctic Waters.* Scientific results of the 'Brategg' Expedition, 1947–48, no. 3, pp. 1–130.

MURRAY Sir J. and HJORT, J. 1912. *The Depths of the Ocean.* London.

RITTER, W. E., 1905. *The pelagic Tunicata of the San Diego region excepting the Larvacea.* Univ. Calif. Pub. Zool. vol. 2, no. 3, pp. 52–113, pls. I–III.

RITTER, W. E. and BYXBEE, EDITH S., 1905. *The pelagic Tunicata. Reports on the Scientific Results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer 'Albatross' from August 1899 to March 1900.* Mem. Mus. Comp. Zool. Harvard, vol. XXVI, no. 5, pp. 195–214.

SARS, MICHAEL, 1829. *Bidrag til Söedyrenes Naturhistorie.* Bergen.

SEWELL, R. B. SEYMOUR, 1926. *The salps of Indian seas.* Rec. Indian Mus. vol. 28, part 2, pp. 65–126.

—— 1953. *The pelagic Tunicata.* Brit. Mus. (Nat. Hist.) John Murray Exped. 1933–34. Sci. Reps. 10 (1), pp. 1–90.

SIGL, M. A., 1912. *Die Thaliacean und Pyrosomen des Mittelmeeres und der Adria.* Denkschr. Akad. Wiss. Wien, vol. LXXXVIII.

STIASNY, G., 1926. *Über die Testa der Salpen und ihre systematische Bedeutung.* Pubb. Staz. zool. Napoli, vol. 7, pp. 385–456.

STREIFF, R., 1908. *Über die Muskulatur der Salpen und ihre systematische Bedeutung.* Zool. Jahrb., Abt. f. Syst., Geog. u. Biol. Tiere, vol. XXVII, no. 1. Jena.

THOMPSON, H., 1948. *Pelagic Tunicates of Australia.* Commonwealth Council for Scientific and Industrial Research, Melbourne. 196 pp., 75 pls.

TOKIOKA, T., 1937. *Notes on Salpas and Doliolums occurring on the Pacific coast of middle Japan.* Annot. zool. jap., vol. XVI, no. 3, pp. 219–36.

TRAUSTEDT, M. P. A., 1885. *Spolia atlantica, 1; Bidrag til kundskab om salperne.* Danske Vid. Sehk. Skrift. vol. 6, part 2, pp. 337–400, pls. I–II.

YOUNT, J. L., 1954. *The taxonomy of the Salpidae (Tunicata) of the central Pacific Ocean.* Pacific Sci. vol. VIII, no. 3, pp. 276–330.

—— 1958. *Distribution and ecologic aspects of central Pacific Salpidae (Tunicata).* Pacific Sci. vol. XII, no. 2, pp. 111–30.

APPENDIX

Stations at which one or other of the four species have been recorded. Unless otherwise stated all are stations worked either by R.R.S. 'Discovery II' or R.R.S. 'William Scoresby' (prefixed by W. S.) and their positions and other data are given in the relevant station lists (Discovery Reports, vols. I, III, IV, XXI, XXII, XXIV, XXV, XXVIII). Station data for material collected by the 'Brategg' Expedition are given in Midttun and Natvig, 1957.

Salpa fusiformis

428, 429, 432–435, 673, 677, 687, 690, 696, 699, 701–708, 710, 711, 713–715, 841, 845–847, 873, 877, 968, 969, 1608–1612, 1736, 1740, 1744, 1756, 1760, 1801–1803, 1806, 2027, 2086, 2148, 2150, 2350, 2380, 2418, 2419, 2453, 2483, 2524, 2526, 2527, 2576, 2683, 2689, 2690, 2691, 2727, 2728, 2731, 2817, 2818, 2889.

Full data for the following stations are unpublished:

	Date	Lat.	Long.
3095 (night)	22. v. 54	44° 49′ N.	16° 13′ W.
3096 (night)	23. v. 54	44° 40′ N.	16° 20′ W.
3097	25. v. 54	44° 44′ N.	16° 40′ W.
3297	15. ix. 55	32° 21′ N.	09° 28½′ W.
3502	28. ii. 57	32° 11′ N.	65° 12′ W.
3508	2. iv. 57	33° 26′ N.	75° 27′ W.
3675	26. iii. 58	28° 02′ N.	16° 55′ W.
3680	1. iv. 58	30° 13½′ N.	15° 59′ W.
3695	7. iv. 58	33° 26′ N.	15° 01′ W.
3700	9. iv. 58	36° 37′ N.	14° 09′ W.

Material from other sources:

	Date	Lat.	Long.
'Sarsia' cruise P6/158. St. 13	13. v. 58	47° 05′ N.	5° 51′ W.
14	14. v. 58	47° 03′ N.	6° 30′ W.
15	14. v. 58	47° 20′ N.	6° 23′ W.
(Dr J. H. Fraser) Haul E57/752	10. ix. 57	63° 51′ N.	16° 20′ W.
(Dr L. Berner)	9. ii. 57	28° 58½′ N.	118° 21·3′ W.
	4. vi. 58	37° 34′ N.	123° 33′ W.
(Professor J. L. Yount)	9. iv. 53	20° 34.6′ N.	157° 32·3′ W.
(Professor T. Tokioka)	3. iii. 36	Seto. Sirahama	
	6. ii. 51	Seto. Sirahama	

Salpa aspera

677, 690, 693, 696, 705, 706, 714, 872, 873, 878, 1612, 1748, 1804, 1806, 2146, 2452, 2457, 2483, 2527, 2683, 2728, 2731, 2820.

Material from other sources:

	Date	Lat.	Long.
(Dr L. Berner)	11. v. 50	32° 04′ N.	118° 12′ W.
	14. v. 57	32° 26′ N.	119° 21′ W.
	4. vi. 58	37° 34′ N.	123° 33′ W.

Salpa thompsoni

168, 171, 176, 197, 198, 199, 201–203, 210, 229, 565, 566, 666, 668, 669, 671, 716–718, 727, 729, 731, 733, 737, 739, 741, 760, 820, 825, 829, 883, 884, 886, 887, 903, 904, 906, 911, 920, 921, 943, 946–948, 951, 958, 959, 964, 971, 1061, 1077, 1098, 1229, 1233, 1235, 1236, 1276, 1295, 1318, 1320, 1326–1333, 1335, 1366, 1442, 1446, 1513, 1515, 1519, 1524, 1545, 1547, 1549, 1550–1552, 1630, 1642, 1792, 1794, 1808, 1827, 1892, 1906, 1912, 2002, 2020, 2087–2091, 2094, 2097, 2100, 2131, 2137, 2144, 2154, 2160, 2177, 2204, 2206, 2209, 2212–2214, 2217, 2220, 2238, 2241, 2258, 2261, 2274, 2277, 2280, 2294, 2311, 2313, 2340, 2457, 2495, 2531–2533, 2574, 2575, 2585, 2620, 2735–2737, 2741, 2769–2771, 2809–2811, 2825, 2826, 2828, 2830, 2835–2837, 2842, 2869, 2875, 2876, W.S. 400, W.S. 401, W.S. 403.

Material from other sources:

	Date	Lat.	Long.
(Dr F. Beyer) 'Brategg' St. 7	16. xii. 57	59° 25′ S.	90° 01′ W.
	2. i. 48.	64° 30′ S.	128° 00′ W.
20	4. i. 48	61° 36′ S.	138° 25′ W.
28	17. i. 48	58° 00′ W.	150° 05′ W.

Salpa gerlachei

1220 1222, 1237, 1239, 1242–1246, 1254–1263, 1269–1271, 1282, 1283, 1286, 1293–1297, 1301, 1306, 1307, 1309, 1311, 1654, 1665, 1667, 2225, 2226, 2228, 2235, 2237, 2240, 2243, 2244, 2246, 2247, 2271, 2743, 2744, 2833.

Material from other sources:

	Date	Lat.	Lond.
(Dr F. Breyer) 'Brategg' St. 15	20. xii. 47	66° 25′ S.	89° 55′ W.
24	16. i. 48	61° 53′ S.	150° 27′ W.
25	17. i. 48	60° 55′ S.	150° 28′ W.
26	17. i. 48	60° 05′ S.	150° 28′ W.